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CONTRIBUTIONS TO PALÆONTOLOGY

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STUDIES OF TERTIARY AND  
QUATERNARY MAMMALS OF  
NORTH AMERICA

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HALL, SCHULTZ, STOCK, WILSON





*C. Louis Geyser*



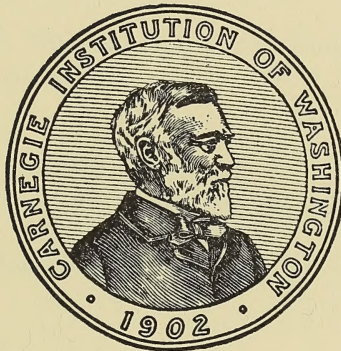


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QUATERNARY MAMMALS  
OF NORTH AMERICA

BY E. RAYMOND HALL, JOHN R. SCHULTZ, CHESTER STOCK,  
ROBERT W. WILSON



PUBLISHED BY CARNEGIE INSTITUTION OF WASHINGTON

1936



CARNEGIE INSTITUTION OF WASHINGTON

PUBLICATION No. 473



JUDD & DETWEILER, INC., PRINTERS  
LANMAN ENGRAVING CO.  
STANDARD ENGRAVING CO.  
WASHINGTON, D. C.



#### LIST OF PAPERS

- I. SCHULTZ, JOHN R.—*Plesippus francescana* (Frick) from the Late Pliocene, Coso Mountains, California, with a Review of the Genus *Plesippus*. Pages 1-13, 3 plates, 3 text-figures. (Issued May 21, 1936.)
- II. WILSON, ROBERT W.—A Pliocene Rodent Fauna from Smiths Valley, Nevada. Pages 15-34, 2 plates. (Issued May 21, 1936.)
- III. STOCK, CHESTER—A Pliomastodon Skull from the Thousand Creek Beds, Northwestern Nevada. Pages 35-39, 1 plate. (Issued May 21, 1936.)
- IV. HALL, E. RAYMOND—Mustelid Mammals from the Pleistocene of North America; with Systematic Notes on Some Recent Members of the Genera *Mustela*, *Taxidea* and *Mephitis*. Pages 41-109, 5 plates, 6 text-figures. (Issued November 20, 1936.)













CONTRIBUTIONS TO PALÆONTOLOGY

I

PLESIPPUS FRANCESCANA (FRICK) FROM THE LATE  
PLIOCENE, COSO MOUNTAINS, CALIFORNIA

With a

REVIEW OF THE GENUS PLESIPPUS

BY JOHN R. SCHULTZ

[Issued May 21, 1936]

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# PLESIPPUS FRANCESCANA (FRICK) FROM THE LATE PLIOCENE, COSO MOUNTAINS, CALIFORNIA

## INTRODUCTION

Two mammalian types, occurring in a late Pliocene fauna from the Coso Mountains, California, have already been described.<sup>1</sup> Among the more abundant forms in this assemblage are the horses of the genus *Plesippus*. These are of particular interest not only for purposes of correlation of the geologic horizon in which they occur, but also because of their phylogenetic relationships. Opportunity is taken therefore to make a comparative study of characters of the species from the Coso Mountains with reference to nearly related forms found in beds of similar age and to define more clearly, than has been previously attempted, the position of *Plesippus* in the lineage of the horse group.

The writer is under obligation to Dr. Chester Stock for opportunity to study the collection, for critical reading of the manuscript, and for his constant interest and guidance during the investigation. Messrs. E. L. Furlong and R. W. Wilson have contributed valuable discussions and suggestions. Thanks are expressed to the Los Angeles Museum for permission to study the mounted specimen of *Plesippus shoshonensis*, and to the U. S. National Museum for loan of material representing this species from Hagerman, Idaho. The type of *Plesippus francescana* was loaned through the kindness of the Museum of Paleontology, University of California. The illustrations have been prepared by Mr. John L. Ridgway.

## LIST OF LOCALITIES

*Calif. Inst. Locality 118*—Immediately north of the Snake River, thirteen miles northwest of Grand View, Ada County, Idaho. (*Plesippus idahoensis*.)

*Calif. Inst. Locality 119*—On south side of the Snake River and opposite locality 118, Owyhee County, Idaho. (*Plesippus idahoensis*.)

*Calif. Inst. Locality 131*—Western flanks of Coso Mountains east of Olancha, Inyo County, California. The Coso Range forms a southward topographical continuation of the Inyo Mountains and bounds the southeastern portion of Owens Valley. (*Plesippus francescana*.)

*Calif. Inst. Locality 210*—U. S. National Museum quarry site on the Snake River near Hagerman, Idaho. (Type of *Plesippus shoshonensis*.)

*Calif. Inst. Locality (unnumbered)*—Valley of Tres Pinos Creek near its junction with Los Muertos Creek, San Benito Quadrangle, California. (*Plesippus proversus*.)

*Univ. of Calif. Locality 2079*—North Coalinga region, western border of the San Joaquin Valley, California, Upper Etchegoin formation. (Type of *Plesippus proversus*.)

<sup>1</sup> R. W. Wilson, Jour. Mammalogy, vol. 13, 150-154, 1932; C. Stock, *ibid.*, vol. 13, 263-266, 1932.

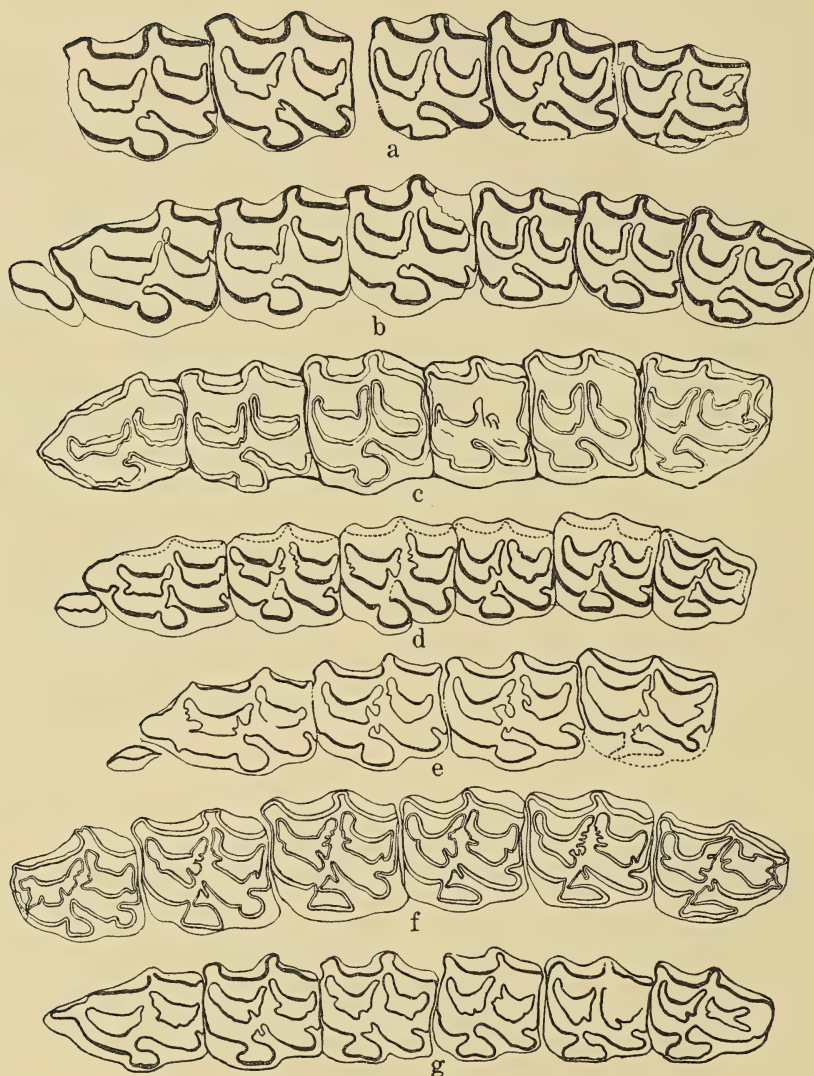


FIG. 1.—Upper cheek-tooth series of species of *Plesippus*. a, type of *P. francescana* (Frick), No. 23277 Univ. of Calif. Coll., Loc. 3253, right side (reversed in printing); b, *P. francescana*, referred specimen, No. 847, Calif. Inst. Loc. 131, right side reversed (in printing); c, *P. simplicidens* (Cope) after Matthew (reversed); d, *P. proversus* (Merriam); e, *P. shoshonensis* Gidley; f, *P. idahoensis* (Merriam), No. 1852, Calif. Inst. Loc. 119; g, *P. idahoensis* (Merriam), No. 892, Calif. Inst. Loc. 118. All figures  $\times \frac{1}{2}$ .



*Univ. of Calif. Locality 3036C*—Near Froman Ferry on the Snake River, eight miles southwest of Caldwell, Idaho, Idaho formation. (Type of *Plesippus idahoensis*.)

*Univ. of Calif. Locality 3253*—Elsinore Quadrangle, central portion of SE  $\frac{1}{4}$  Sec. 9, T. 3S, R. 2W., Upper San Timoteo beds. (Type of *Plesippus francescana*.)

*Univ. of Texas*—Crosby County, Texas, Blanco Canyon bed. (Type of *Plesippus simplicidens*.)

*Univ. of Texas*—Mont Blanco, Crosby County, Texas, Blanco formation. (Type of *Plesippus cummingsii*.)

#### *Plesippus francescana* (Frick)

Although no complete skulls were found, the collection from the late Pliocene beds of the Coso Mountains includes several series of upper and lower teeth, jaws, and numerous skeletal elements. Comparison with specimens of *Pliohippus francescana* Frick from the San Timoteo beds of southern California fails to disclose any difference except that of size. Consequently the material from the Coso Mountains is referred to Frick's species. The collection now available permits a supplementary description of this form. Additional characters are: (1) presence of a large and functional P<sub>1</sub>, (2) nearly vertical position of the upper incisors, (3) flattening of the protocone in the last two premolars, (4) presence of a vestigial protostylid in individual lower cheek-teeth, (5) characters of the milk dentition. Reasons for referring the species to *Plesippus* rather than to *Pliohippus* will be more fully discussed elsewhere in this paper.

#### DESCRIPTION OF MATERIAL

*Material*—A mandible, No. 902 (Plate 1); a series of upper cheek-teeth, No. 847 (Plate 2, fig. 2); three upper milk teeth, No. 1847 (Plate 2, figs. 3 and 4); three lower milk teeth, No. 1848 (Plate 2, fig. 1); numerous fragmentary mandibular rami and maxillaries; various limb elements. All specimens in the collection of the California Institute of Technology and from Calif. Inst. Tech. Vert. Pale. Locality 131.

*General Characters of Skull and Dentition*—The mandibular specimens indicate a form of large size, comparable in this character to *Equus caballus*. The cheek-teeth are long with moderately curved and well-cemented crowns. The incisors have a procumbent position approximately like that in the modern genus. A large and functional P<sub>1</sub> is always present. Since a detailed description of the permanent cheek-teeth would merely result in a repetition of Frick's exposition,<sup>1</sup> it has been omitted.

*Upper Deciduous Cheek-Teeth*—In these teeth the parastyles are larger and flatter than the mesostyles. The external borders of the fossettes are round. Both fossettes are moderately broad, and their borders show few plications. A well-developed posthypoconal valley lends an oval shape to the hypocone in Dp<sub>2</sub> and Dp<sub>3</sub>, and an irregular, pointed outline to this cusp in Dp<sub>4</sub>. The protocone approximates an oval in shape in Dp<sub>2</sub>, but is flattened and is slightly indented in the remaining milk-teeth. A single pli caballin is present. For illustrations see Plate 2, figures 3 and 4.

*Lower Deciduous Cheek-Teeth*—A striking feature is the presence of an anteroexternal enamel fold (protostylid) on the protoconid. A similar fold

<sup>1</sup> Childs Frick, Univ. Calif. Pub., Bull. Dept. Geol., vol. 12, 322-333, 1921.

is present in lower milk teeth of *Plesippus shoshonensis*. It is probable that a protostylid will be found in deciduous teeth of allied species of *Plesippus*, since it occurs in milk-teeth of *Equus occidentalis*. A vestige of this fold is present in permanent teeth of some species of *Pliohippus*<sup>1</sup> and in *Plesippus simplicidens*<sup>2</sup> and *P. francescana*.

The external walls of the protoconid and hypoconid are convex. A single subsidiary fold marks the posterior, internal border of the median external valley. The valley extends approximately one-third of the distance from the outer side of the internal groove in Dp2̄, very nearly to the gutter in Dp3̄, and touches the enamel of this groove in Dp4̄. The gutter is sharply V-shaped in Dp2̄, but is broader and less deeply incised in the remaining teeth. The metastylid is nearly oval in shape in Dp2̄, and approaches the

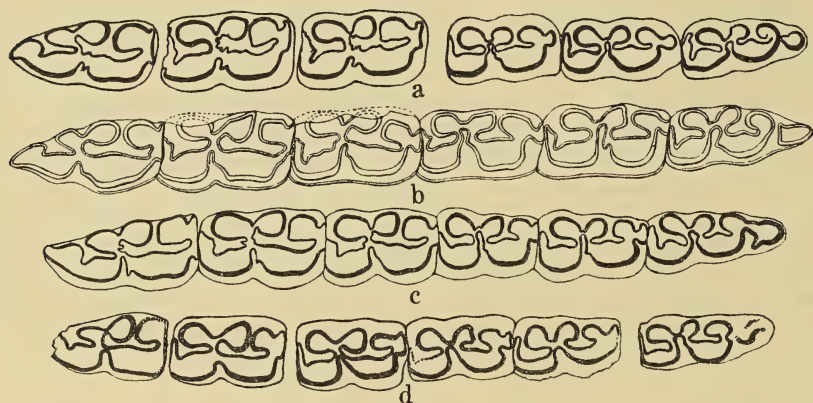


FIG. 2—Lower cheek-tooth series of *Plesippus*. a, *P. francescana* (Frick), No. 902, Calif. Inst. Loc. 131; b, *P. simplicidens* (Cope), after Cope; c, *P. shoshonensis* Gidley, No. 1581, Calif. Inst. Loc. 210; d, *P. idahoensis* (Merriam), No. 892, Calif. Inst. Loc. 118. All figures  $\times \frac{1}{2}$ .

metaconid in size, but is smaller than this cusp in the posterior teeth. A markedly rounded outline characterizes the entoconid. The hypoconulid is expanded transversely both internally and externally in Dp4̄, very slightly internally and very greatly externally in Dp3̄, and only internally in Dp2̄. These teeth are illustrated in Plate 2, figure 1.

**Limb and Foot Elements**—The distal ends of the tibia and fibula are fused as completely as in the modern species. Carpals and tarsals are more slender than the corresponding elements in *E. caballus*. The metapodials are relatively slender, but approach in their proportions those of the living form. None of the lateral digits is complete at the distal end, but it is probable that these elements did not extend more than three-quarters of the length of the cannon bone. The ungual phalanges are small (see Plate 3).

**Measurements**—The following measurements are taken according to the system employed by Merriam.<sup>3</sup> Specimen No. 1846 is worn slightly more than No. 847.

<sup>1</sup> H. F. Osborn, Mem. Amer. Mus., n. s., vol. 2, pt. 1, 146, 1918.

<sup>2</sup> J. W. Gidley, Bull. Amer. Mus., vol. 14, 125, 1901.

<sup>3</sup> J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 7, 409, 1913.



## Measurements (in millimeters)

## PERMANENT DENTITION

	No. 847	No. 1846
Length of upper molar-premolar series with P <sub>1</sub> .....	201	.....
Length of upper premolar series without P <sub>1</sub> .....	104	.....
Length of upper molar series.....	84	83.5
P <sub>2</sub> anteroposterior diameter.....	40.8	.....
P <sub>2</sub> transverse diameter.....	30.4	.....
P <sub>3</sub> anteroposterior diameter.....	32.8	31
P <sub>3</sub> transverse diameter.....	32	35.4
P <sub>4</sub> anteroposterior diameter.....	31.3	30
P <sub>4</sub> transverse diameter.....	31	33.5
M <sub>1</sub> anteroposterior diameter.....	25	23.4
M <sub>1</sub> transverse diameter.....	27.2	31.2
M <sub>2</sub> anteroposterior diameter.....	26	28.5
M <sub>2</sub> transverse diameter.....	28	30
M <sub>3</sub> anteroposterior diameter.....	32.3	31.6
M <sub>3</sub> transverse diameter.....	25.6	27.5

	No. 849	No. 902
Length of lower molar series.....	89	91
Length of lower premolar series.....	.....	102
P <sub>2</sub> anteroposterior diameter.....	.....	36.8
P <sub>2</sub> transverse diameter.....	.....	16.5
P <sub>3</sub> anteroposterior diameter.....	32.2	32.8
P <sub>3</sub> transverse diameter.....	16	17
P <sub>4</sub> anteroposterior diameter.....	31.8	32.8
P <sub>4</sub> transverse diameter.....	15.3	16.8
M <sub>1</sub> anteroposterior diameter.....	28.7	27.8
M <sub>1</sub> transverse diameter.....	13.8	14.8
M <sub>2</sub> anteroposterior diameter.....	29	29.8
M <sub>2</sub> transverse diameter.....	13.2	13.8
M <sub>3</sub> anteroposterior diameter.....	31	31.4
M <sub>3</sub> transverse diameter.....	10	12.8
I <sub>1</sub> greatest transverse diameter.....	.....	9.5
I <sub>2</sub> greatest transverse diameter.....	.....	9.5
C greatest anteroposterior diameter.....	.....	14

## MILK DENTITION

	No. 1847
Dp <sub>2</sub> anteroposterior diameter.....	.....
Dp <sub>2</sub> transverse diameter.....	22.4
Dp <sub>3</sub> anteroposterior diameter.....	33
Dp <sub>3</sub> transverse diameter.....	21.6
Dp <sub>4</sub> anteroposterior diameter.....	34
Dp <sub>4</sub> transverse diameter.....	22.6
Dp <sub>4</sub> length of crown.....	41
	No. 1848
Dp <sub>2</sub> anteroposterior diameter.....	38
Dp <sub>2</sub> transverse diameter.....	13.4
Dp <sub>3</sub> anteroposterior diameter.....	33
Dp <sub>3</sub> transverse diameter.....	13.3
Dp <sub>4</sub> anteroposterior diameter.....	34
Dp <sub>4</sub> transverse diameter.....	13.2

## ADDITIONAL SPECIES REFERRED TO PLESIPPUS

*Plesippus simplicidens* (Cope) <sup>1</sup>—Figures 1c and 2b illustrate the characters of the upper and lower cheek-tooth series of this species. The type was originally assigned to *Equis*, but was referred to *Pliohippus* by Gidley.<sup>2</sup> Matthew<sup>3</sup> on the basis of material referred to this species, established the genus *Plesippus*.

<sup>1</sup> E. D. Cope, Proc. Amer. Philos. Soc., vol. 30, 124-125, 1892.

<sup>2</sup> J. W. Gidley, Bull. Amer. Mus., vol. 14, 125, 1901.

<sup>3</sup> W. D. Matthew, Amer. Mus. Novitates, No. 131, 1924.

*Plesippus cumminsii* (Cope) <sup>1</sup>—This species is based on very fragmentary material. It appears to be closely related to *P. simplicidens*, and, following Matthew and Stirton,<sup>2</sup> may readily be referred to the same genus. Both forms were described from the Blanco beds of Texas.

*Plesippus proversus* (Merriam) <sup>3</sup>—This species, based on several upper and lower teeth, was described by Merriam from the Upper Etchegoin horizon of California. Merriam assigned the species to *Pliohippus*, but appreciated the advanced characters of the type as implied by the specific name. The form was later referred to *Plesippus* by Matthew.<sup>4</sup> Since this description the same species has been recognized by Russell and Vander Hoof<sup>5</sup> in a late Pliocene mammalian fauna from northern California. The tooth-row illustrated in figure 1d belongs to a skull of *Plesippus proversus* embedded in a boulder found in a stream bed several miles south of Hollister, San Benito County, California. Unfortunately the source of the boulder is not determined.

Additional tooth-characters furnished by this new material are: (1) a rather marked anterior projection of the protocone in all teeth except P<sub>2</sub>, (2) the flattened or indented inner wall of the protocone in the cheek-teeth, except in the second and fourth upper premolars, (3) moderate width of the isthmus except in P<sub>4</sub> where it is noticeably wider, and (4) presence of a functional P<sub>1</sub>.

*Plesippus shoshonensis* Gidley <sup>6</sup>—Figure 1e shows the pattern of the upper dentition of No. 1863 from the Hagerman locality in Idaho, while figure 2c illustrates the lower tooth-row of specimen No. 1581, Calif. Inst. Tech. Vert. Pale. Coll. from the same locality. Moderately worn upper molars exhibit greatly elongated protocones, the inner margins of which are flattened but not indented. The anterior projection of this cusp beyond the level of the isthmus is marked. The isthmus is usually quite narrow.

In the lower cheek-tooth series, the proto- and hypoconids are moderately flattened in the premolars; in the molar series, however, these pillars are markedly rounded. The internal groove or gutter is sharply V-shaped at its outermost extremity, but is seen to broaden out rapidly toward the median plane of the jaw.

A palate and dentition of a young individual of *P. shoshonensis*, No. 1783, shows the protocone to be somewhat flattened and indented in the milk-teeth. An interesting feature of this specimen is the union of the post-protoconal valley and prefossette. Individual lower milk-teeth possess a well-developed protostylid; one specimen, No. 1851 (fig. 3b), shows the presence of a posterior, external fold (hypostylid).

*Plesippus idahoensis* (Merriam) <sup>7</sup>—*Equus idahoensis* was described on the basis of two teeth found near Froman Ferry on the Snake River, Idaho. Specimen No. 892 (figs. 1g, 2d) representing a fragmentary skull with dentition, found near Grand View, Idaho, C.I.T. Locality 118, is referred to this species. The skull proportions are similar to those in *E. caballus*. P<sub>1</sub> is represented by a vestige on the right side of the palate. The protocone

<sup>1</sup> E. D. Cope, 4th Ann. Rept. Geol. Surv. Texas, 67, 1893.

<sup>2</sup> W. D. Matthew and R. A. Stirton, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 19, 359, 1930.

<sup>3</sup> J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 9, 525-534, 1916.

<sup>4</sup> W. D. Matthew, *op. cit.* 2, 1924.

<sup>5</sup> R. D. Russell and V. L. Vander Hoof, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 20, 17-19, 1931.

<sup>6</sup> J. W. Gidley, Jour. Mammalogy, vol. 11, 300-301, 1930.

<sup>7</sup> J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 10, 527-530, 1918.

## KEY TO SPECIES OF PLESIPPUS

	FRANCESCANA	SIMPLICIDENS	PROVERSUS	SHOSHONENSIS	IDAHOENSIS
PROTOCONE	Usually flat, very slight indentation and projection. Length moderate.	Flat. Very little indentation. Projects only in molars. Length moderate.	Flat and moderately indented. Projection moderate.	Flat. Seldom indented. Projection marked. Length great.	Flat. May or may not be indented, but usually markedly so. Projection moderate to great. Length moderate to great.
CURVATURE	Marked to moderate.	Moderate.	Moderate.	Very moderate.	Nearly straight.
FOSSETTES	Moderately broad. Plications few.	Moderately broad. Plications few.	Large moderately complicated borders.	Moderately broad. Borders moderately complicated.	Large, complicated.
PROTO- AND HYPOCONID	Convex. Protostylid vestigial.	Slightly flat. More nearly round in molars. Protostylid vestigial.	Convex to slightly flat.	Convex to flat Hypoconid usually the flatter.	Nearly flat in the premolars. More nearly round in the molars.
GUTTER	Sharp V in premolars. Apex flat in molars.	Wide but pointed at apex.	Round V to open.	V-shaped.	V-shaped to broadly open in premolars.



shows a marked anterior projection in all teeth except in P2. The very slight indentation of the inner wall of this cusp is largely the result of an advanced stage of wear.

The protoconid and hypoconid have rounded faces in the molars, but these are noticeably flattened in the premolars. The metaconid-metastylid groove opens more widely in the premolars than in the molars. In the latter it forms a V-shaped incision.

A single specimen, No. 1852 (fig. 1f), from C. I. T. locality 119 near Grand View, Idaho, is doubtfully referred to this species. The major differences between this specimen and No. 892 are: (1) narrower isthmus, and (2) less-marked indentation of inner wall of protocone and shorter anterior projection of this cusp. These differences appear to be due principally to individual variation, since both specimens show approximately the same stage of wear. These two individuals appear to be closely related and may be specifically identical. Reasons for referring the species to *Plesippus* rather than to *Equus* are given at the end of the following section.

### STATUS OF THE GENUS PLESIPPUS

If controversial species, here assigned to *Plesippus*, are excluded from *Pliohippus*, the latter genus is characterized by the following tooth characters:<sup>1</sup> (1) cheek-teeth strongly incurved, (2) isthmus broad in upper cheek-teeth, (3) protocone round-oval in shape, (4) pre- and postfossettes broad, enamel borders with few or no plications, (5) outer walls of protoconid and hypoconid rounded, (6) metaconid-metastylid gutter sharply V-shaped.

Excluding from *Equus* those species that are referred to *Plesippus*, we note that the former genus possesses the following characters: (1) cheek-teeth with nearly straight crowns, (2) isthmus narrow, (3) protocone elongated, indented, and with marked anterior projection, (4) borders of pre- and postfossettes usually with numerous plications, (5) proto- and hypoconids with flattened or slightly concave external walls, (6) metaconid-metastylid groove broadly open.

The striking feature of the forms assigned to *Plesippus* is that they partake individually of both *Pliohippus* and *Equus* characters. Among these species some show considerable resemblance to *Pliohippus*, while others approximate in their characters the genus *Equus*. The intermediate types of the series can be assigned with equal right to either genus. Recognizing *Plesippus* as a subgenus of *Equus*, as Stirton<sup>2</sup> has done, has the disadvantage of vitiating the unity of characters which defines the latter genus, while an assignment to *Pliohippus* likewise destroys the unity of characters of that genus. Determination of border-line species in the classification would still remain a difficult task. However, this difficulty can not be entirely removed by any classification. If, on the other hand, the intermediate position of *Plesippus* is recognized, proper generic reference of end members becomes a matter of considerably less importance. Total elimination of the genus would merely serve to raise the objections stated above, but to a still more marked degree.

Intergradation of specific and generic characters has been discussed recently by Bode,<sup>3</sup> who has shown that recognition of this fact is a natural

<sup>1</sup> Slightly modified after H. F. Osborn, *op. cit.* 146, 1918.

<sup>2</sup> R. A. Stirton, Cordilleran Sec. G. S. A., 33d Ann. Meeting, 37, 1934.

<sup>3</sup> F. D. Bode, Carnegie Inst. Wash. Pub. No. 453, 61-63, 1934.

outcome of increased knowledge of fossil faunas. It is to be expected that certain genera are intermediate in their structural features, but this fact alone does not imply necessarily that a particular genus is invalid, for if the complete fossil record of a family were known all genera would presumably grade into each other. Where genera are to be recognized at all, they must be defined so as to emphasize relationships. In view of these considerations it appears advisable to retain *Plesippus* in full generic rank, and to assign to the genus all species possessing characters of both *Pliohippus* and *Equus*.

*P. francescana* has been transferred from *Pliohippus* to *Plesippus* for the following reasons. In the upper teeth the characters of the fossettes are typically *Pliohippus*-like. The protocones, however, show some of the characters of *Equus*, for example, their great length, slight anterior projection beyond the isthmus, and slight indentation of their inner faces. The lower teeth resemble those of *Pliohippus* in all details except the flattening of the hypoconid in the premolars.

*Equus idahoensis*, on the other hand, has been assigned to *Plesippus* principally because, notwithstanding the characters of the upper teeth which resemble those of *Equus*, the lower dentition retains many *Pliohippus* characters. Among these are: the V-shaped metaconid-metastylid groove and the more or less convex faces of the proto- and hypoconids.

### ANCESTRY OF THE EQUUS

The illustrations of the series of cheek-teeth of the several species of *Plesippus* (figs. 1 and 2) show a striking gradation of characters from *Pliohippus* to *Equus*. Moreover, the occurrence of *Plesippus* in the late Pliocene and possibly early Pleistocene is in accord with the intermediate position which this form holds between the latter genera. It seems apparent that the gradation in characters indicates a relationship between the Pliocene *Pliohippus* and Pleistocene *Equus*. Retention of an intermediate genus, namely *Plesippus*, therefore marks that genus as an ancestor of *Equus*.

The characters in the dentition of *Pliohippus* are quite constant as are likewise those in various species of *Equus*. Examination of a large series of specimens of *E. occidentalis* from the McKittrick Pleistocene of California reveals the fact that while minor variations occur, much less individual difference exists among these forms than among either *Plesippus francescana* or *P. idahoensis*. An inference may be drawn that the tooth-characters of *Plesippus* were in a mobile or unstable state, possibly the result of rather rapid evolution of the group.

Whether this development in time was directional and marked by gradual and progressive modification of essential dental characters, or whether it was a more or less random process, can not be definitely determined at present. With regard to the material at hand, it is important to recognize that in all cases the lower premolars are more advanced than the molars. This is not only true for the specimens figured, but has been observed in all the material studied. The illustrations, figures 1 and 2, are arranged in an attempt to show the probable phylogenetic sequence. Not all of the evidence supports this arrangement. Thus, as mentioned on a preceding page, the pre-fossette is united with the post-protoconal valley in milk-teeth of *P. shoshonensis*, while the two are separate in deciduous teeth of *P. francescana*. On this character alone *P. shoshonensis* would appear to be a more primitive type than *P. francescana*. On the other hand, the



structural features of the permanent dentition seemingly indicate that *P. shoshonensis* is more advanced. This conflicting evidence tends to cast doubt on the assumption that evolution was progressive in all characters, and practically eliminates the possibility of constructing a satisfactory phylogenetic chart.

With reference to possible correlation of the instability of characters seen in the *Plesippus* group with rapidly changing environmental conditions, it should be mentioned that the late Pliocene marks a time of critical conditions immediately antecedent to the coming of the Ice Age.

## PLESIPPUS-LIKE TYPES OF EURASIA AND NORTHERN AFRICA

Boule<sup>1</sup> has shown that the European *Equus stenonis* of the late Pliocene and early Pleistocene comprises two quite diverse types. According to this author the first or *Equus caballus* type is characterized by long, indented protocones, complicated fossette borders, and large and fluted styles in the upper dentition; the second or *E. stenonis* type is characterized by teeth possessing shorter protocones, which are not indented and which do not project so far anteriorly. This form is further distinguished by simple fossette borders, and smaller, non-bifurcate styles. In the lower dentition

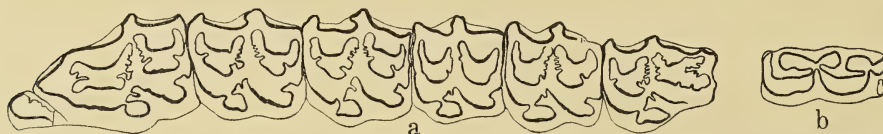


FIG 3—a, *Equus? stenonis* Cocchi, after Forsyth Major; b, *P. shoshonensis* Gidley, lower milk tooth, No. 1851, Calif. Inst. Loc. 210.  $\times \frac{1}{2}$ .

the protoconid and hypoconid are rounded as are also the metaconid and metastylid, and the latter are separated by a V-shaped notch. Figure 3a illustrates the characters of this group.

It is apparent that the dental characters of the *E. stenonis* type correspond almost exactly with those of *Plesippus*, as defined on pages 10–11 of this paper. On the other hand, those of the *E. caballus* type are more like the characters seen in North American horses of the later Pleistocene. The bifurcation of the styles does not appear to be a constant character among North American species of *Equus*. It would appear, therefore, that this feature possesses little diagnostic value. However, the styles are never bifurcate in *Plesippus*.

Another character pointed out by Boule is the presence of a postero-external cuspule (hypostylid) in lower milk-teeth of *E. stenonis* and of closely related forms, *E. asinus atlanticus* and *E. burchelli*. This cuspule is absent in deciduous teeth of *E. asinus* and *E. caballus*. Boule<sup>2</sup> concluded that *E. stenonis* gave rise to *E. caballus* (not to be confused with the *E. caballus* type or subspecies of *E. stenonis*), while a persistently primitive branch of the same species, i.e. *E. stenonis*, is represented by the modern zebra. He also concluded that the Pleistocene forms of Europe are all of the *E. caballus* type, and that the ancestor of the European *E. stenonis* is to be found in *Protohippus* of North America.<sup>3</sup>

<sup>1</sup> Marcellin Boule, Bull. Soc. Géol. de France, Ser. 3, vol. 27, 531–542, 1899.

<sup>2</sup> M. Boule, *op. cit.* 532, 534, 542, 1899.

<sup>3</sup> M. Boule, Annales de Paléontologie, Tome 5, 18, 1910.



Figure 3b illustrates a lower milk molar, No. 1851 from C. I. T. Locality 210, of *Plesippus shoshonensis*. The feature of particular interest about this tooth is the presence of a hypostylid similar to that described by Boule in milk-teeth of *E. stenonis* and of related forms. This evidence in addition to that already discussed, suggests that the *E. stenonis* type, as defined by Boule from the late Pliocene of Europe, falls within the *Plesippus* group of North America, and is perhaps a descendant of some species of the latter genus. In other words, the differences between the two European types grouped under a single species, namely *E. stenonis*, are here considered to be of generic value. Boule's *E. stenonis* type from the late Pliocene of Europe becomes *Plesippus stenonis*, while his *E. caballus* type from the European early Pleistocene is retained in *Equus*, and may be designated *Equus stenonis*.

In this connection it should be noted that *E. sivalensis* of the Siwalik beds of India was regarded by Forsyth Major<sup>1</sup> as identical with *E. stenonis*. Judging from Lydekker's remarks,<sup>2</sup> one may conclude that *E. sivalensis* is allied with the true *Equus* rather than with the *Plesippus* group. *E. stenonis* is found also in the late Pliocene Norwich Crag of England.<sup>3</sup> These deposits contain *Miomys*, a genus of vole closely related to *Cosomys* of the Coso Mountains. No illustrations of *E. stenonis* from the Norwich Crag are available, but it is inferred that this species belongs to the *Plesippus* group. Recognition of the primitive forms of *E. stenonis* as *Plesippus* may facilitate late Tertiary and early Pleistocene correlation between Eurasia, Northern Africa,<sup>4</sup> and North America, as well as aid in establishing a fairly sharp faunal demarcation between the two periods.

It is interesting to recall that Merriam<sup>5</sup> suggested a possible relation of *Plesippus proversus* from the Upper Etchegoin of California to *Equus stenonis* of the Old World. He considered the time represented by the late Pliocene or early Pleistocene Tulare beds of California as sufficient to permit migration from North America to Europe.

In a recent paper, Colbert<sup>6</sup> regards *Plesippus* as intermediate between *Plihippus* and *Equus*, and expresses the view that the *Equus* forms of the Upper Siwalik are derived from North American ancestors. Colbert concludes that since the first appearance of *Equus* in North America is at the base of the Pleistocene, the Upper Siwalik is Pleistocene in age.

<sup>1</sup> C. J. Forsyth Major, Quart. Jour. Geol. Soc. London, vol. 41, 3, 1885.

<sup>2</sup> R. Lydekker, Palæontologia Indica, Ser. X, vol. 2, plates XIV, XV, 1881-84.

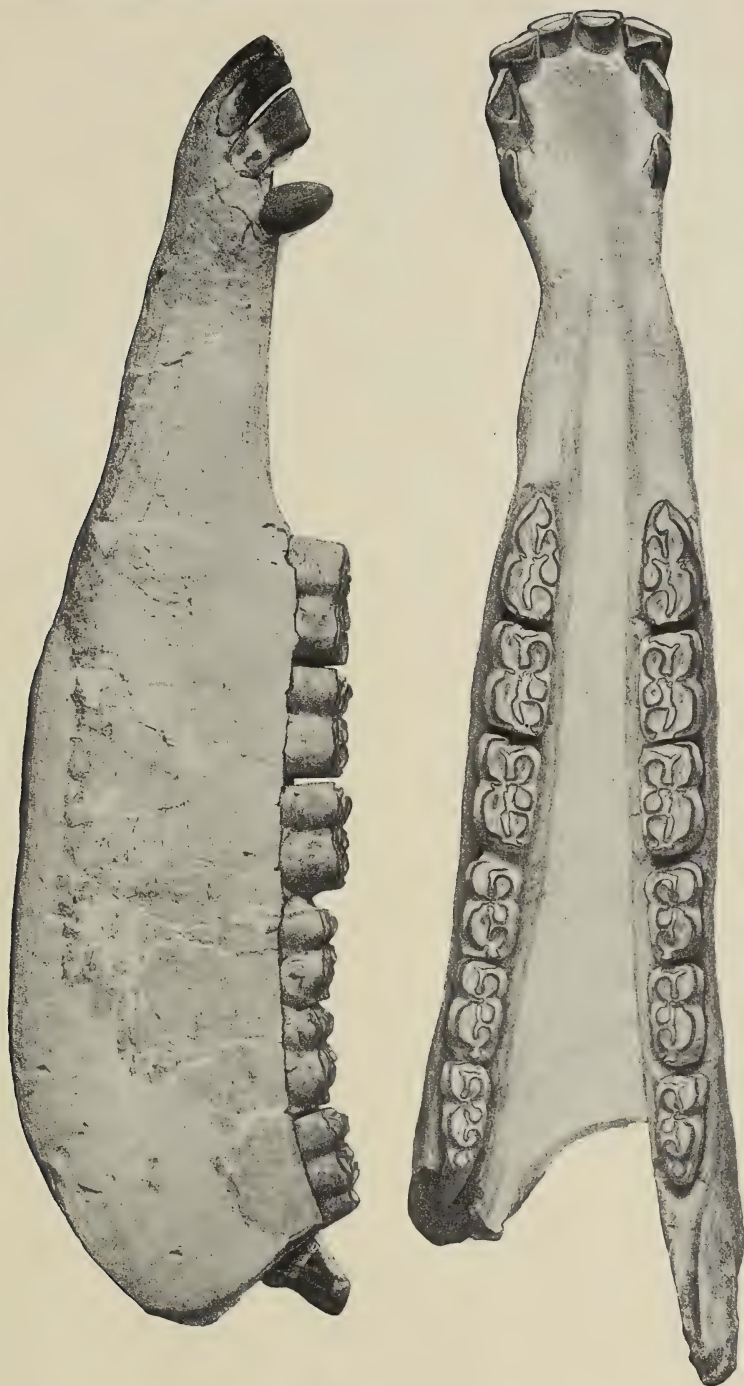
<sup>3</sup> J. W. Evans and C. J. Stubblefield, Handbook of the Geol. of Great Britain, 435, 1929.

<sup>4</sup> R. Lydekker, Quart. Jour. Geol. Soc. London, vol. 43, 161-163, 1887.

<sup>5</sup> J. C. Merriam, *op. cit.* 532-533, 1916.

<sup>6</sup> E. H. Colbert, Amer. Mus. Nat. Hist. Novitates, No. 797, 11-12, 1935.





*Plesippus francescana* (Frick)

No. 902, mandible, lateral and occlusal views. The symphyseal end has been bent a trifle downward. Approx. 2/5 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Pliocene, Coso Mountains, Calif.





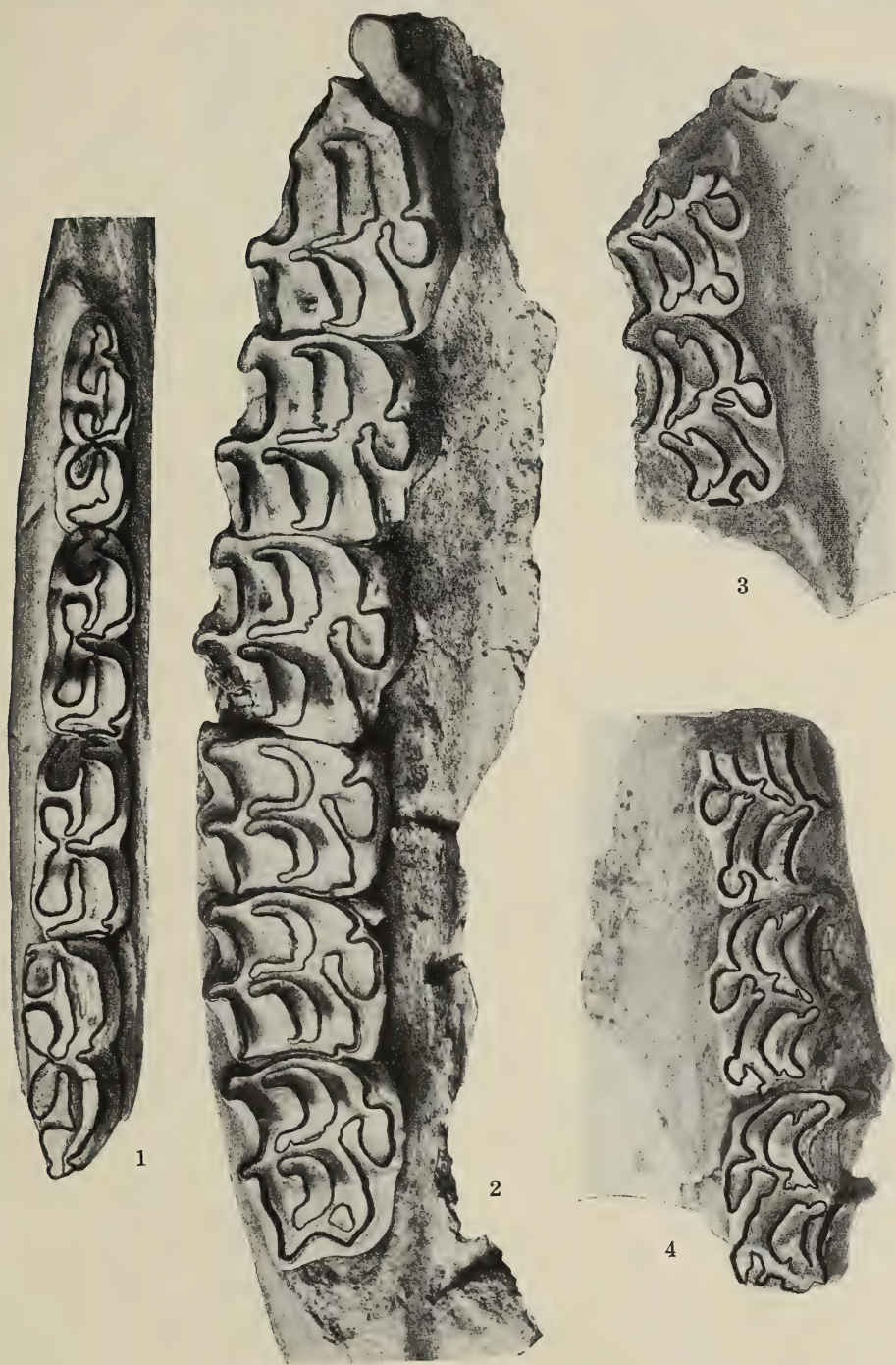
*Plesippus francescana* (Frick)

FIG. 1—Left ramus with Dp $\bar{2}$ – $\bar{4}$  and M $\bar{1}$ , No. 1848.

FIG. 2—Deeply worn upper cheek-tooth series, No. 847.

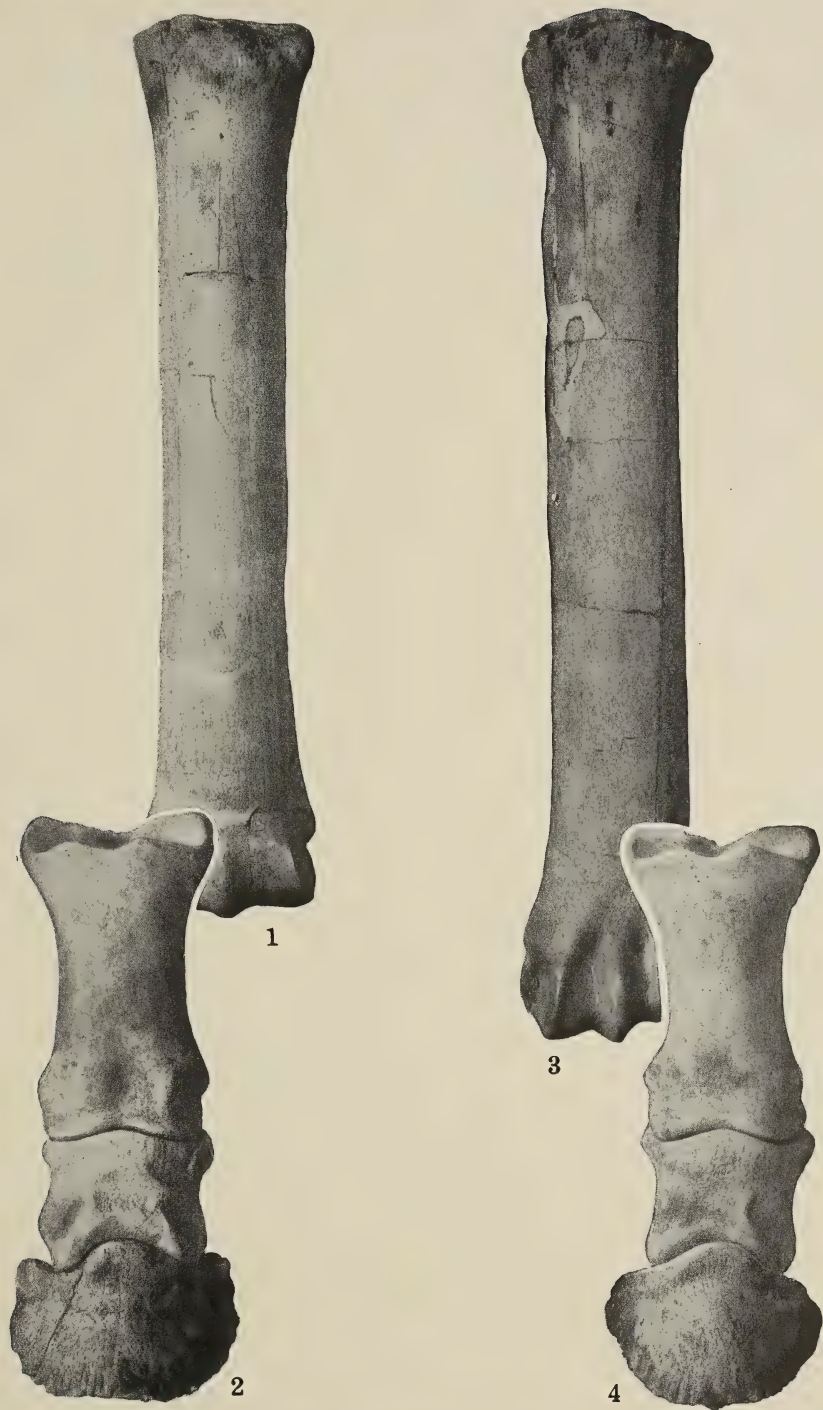
FIGS. 3, 4—Dp $\bar{2}$ , Dp $\bar{3}$  of right side and Dp $\bar{2}$ – $\bar{4}$  of left side, No. 1847.

All figures approx. 4/5 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Pliocene, Coso Mountains, Calif.







*Plesippus francescana* (Frick)

FIG. 1—Right metacarpal III, No. 1924.

FIG. 3—Right metatarsal III, No. 1923.

FIG. 2—Phalanges, Nos. 1925, 1926, 1927.

FIG. 4—Phalanges, Nos. 1928, 1929, 1930.

All figures 1/2 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Pliocene, Coso Mountains, Calif.









CONTRIBUTIONS TO PALÆONTOLOGY

II

A PLIOCENE RODENT FAUNA FROM SMITHS  
VALLEY, NEVADA

By ROBERT W. WILSON

With two plates

[Issued May 21, 1936]

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# A PLIOCENE RODENT FAUNA FROM SMITHS VALLEY, NEVADA

## INTRODUCTION

Tertiary mammalian remains were discovered by Chester Stock and E. L. Furlong several years ago in sedimentary beds exposed along the eastern side of Smiths Valley and south of Wilson Canyon, west-central Nevada. Since then field explorations have been conducted in the region, during the summers of 1931 and 1934, by the California Institute of Technology. At one locality near the western mouth of Wilson Canyon and about fifteen miles airline from Yerington, a small collection of rodent remains was obtained, the description of which is the purpose of the present paper.

Determination of Pliocene age for the deposits is afforded, chiefly, by the larger mammals in the fauna, especially the Equidæ. However, the rodent assemblage is suggestive of a similar age and indeed in one or two points indicates a stage of evolution approximating the Thousand Creek middle Pliocene fauna from northwestern Nevada.

The author wishes to acknowledge the kindness of the Museum of Paleontology, University of California, in loaning fossil rodent material from Fish Lake Valley and Thousand Creek deposits. The illustrations reproduced herein are from photographs which have been carefully retouched and arranged by Mr. John L. Ridgway.

## COMPARISON OF THE PLIOCENE RODENTS AND LAGOMORPHS OF SMITHS VALLEY AND THOUSAND CREEK

While the actual number of rodent specimens found at the Smiths Valley and Thousand Creek localities are not far different, the limited collecting area at the former locality has served perhaps to restrict the number of distinct types. Hence, comparison of the two faunas is handicapped by lack of similar rodent groups.

Among the sciuromorphs, the Smiths Valley aplodontid is too fragmentary to be of correlative value, except to indicate a Pliocene age for the fauna. *Citellus?* species possibly represents a stage of evolution comparable to *Citellus* species from Thousand Creek, but neither species is specifically determinable, and the dentition of the Sciuridæ is apparently too stable to be of much service in correlation. *Pliosacomys* may have a counterpart in the Thousand Creek co-type of *Cupidinimus magnus*, but the relation of the former to the latter can not be satisfactorily established on the basis of available Thousand Creek material. The Thousand Creek genera *Mylagaulus*, *Marmota*, *Dipoides* and *Diprionomys* are not represented in the Smiths Valley assemblage, but the absence of *Mylagaulus*, at least, is certainly fortuitous.

In the myomorph group, *Peromyscus* near *antiquus* is very close to, if not identical with, the Thousand Creek species. Neither *Pliozapus* nor any zapodid is represented in the Thousand Creek fauna.

The Smiths Valley leporid represents a smaller species of lagomorph than *Hypolagus vetus*, but this does not necessarily indicate a less advanced form, as small leporids are known from the upper Pliocene.

R. A. Stirton described and figured<sup>1</sup> two isolated beaver teeth as *Eucastor* cf. *lecontei* from beds seventeen miles south of Yerington, Nevada. In view of the fact that a more advanced member of the same phylum, namely *Dipoides*, is known from Thousand Creek, it should be pointed out that the fossil beaver locality is in another basin some distance to the east of the Smiths Valley locality, and may come from beds representing a different time stage.

It seems desirable to call attention to the fact that the Thousand Creek rodent assemblage, and to a lesser extent that from Smiths Valley, shows a predominance of sciuromorph types characteristic of the North American Tertiary up to the upper Pliocene. In the upper Pliocene (cf. faunas of Grand View, Hagerman, Benson and Curtis), however, the myomorph group becomes for the first time an important element in the assemblage.

Comparative faunal lists of Smiths Valley and Thousand Creek are given below.

SMITHS VALLEY	THOUSAND CREEK
Rodentia	Rodentia
<i>Aplodontid</i> species	<i>Mylagaulus</i> cf. <i>monodon</i> Cope
	<i>Liodontia furlongi</i> Gazin
	<i>Marmota nevadensis</i> (Kellogg)
	<i>Marmota minor</i> (Kellogg)
<i>Citellus?</i> species	<i>Citellus</i> species
	<i>Dipoides</i> species
	<i>Diprionomys parvus</i> Kellogg
	<i>Cupidininus magnus</i> (Kellogg)
<i>Pliosacomys dubius</i> n. gen. and sp.	
<i>Pliozapus solus</i> n. gen. and sp.	
<i>Peromyscus</i> near <i>antiquus</i> Kellogg	<i>Peromyscus antiquus</i> Kellogg
Lagomorpha	Lagomorpha
<i>Leporid</i> species	<i>Hypolagus vetus</i> (Kellogg)

## SYSTEMATIC DESCRIPTION OF SPECIES

### APLODONTIIDÆ

#### *Aplodontid* species

The outer half of a left P4, Calif. Inst. Tech. Coll. Vert. Pale. No. 1793, is referred to an aplodont rodent. The styles are prominent and acute. A slight and discontinuous coating of cement? is present on the tooth. No

<sup>1</sup> R. A. Stirton, Univ. Calif. Pub., Bull. Dept. Geol. Sci., Vol. 23, No. 13, 439, figs. 117-118, 1935.

indication of the presence of lakes is seen in the fragment preserved. In acuteness of outer styles, the Smiths Valley specimen resembles more closely Thousand Creek specimens of *Liodontia furlongi* than it does *L. alexandræ* from the Virgin Valley middle Miocene deposits. Apparently, no characters are present that would serve to distinguish our specimen from Thousand Creek aplodonts.

## SCIURIDÆ

### *Citellus?* species

A small sciurid species is represented principally by a right lower jaw without teeth, Calif. Inst. Tech. Coll. Vert. Pale. No. 1795, and a fragment of left ramus with M<sub>2</sub>, C.I.T. No. 1794 (Plate 1, fig. 5).

No. 1794 shows several characters which indicate its intermediate character between *Sciurus* and typical citellids, as for example *Citellus armatus*. Thus it may be allocated to the group of ground-squirrels with relatively unspecialized dentition, which includes *Callospermophilus* and *Citellus* (*Otospermophilus*).

M<sub>2</sub> has a basin which is rather compressed in fore and aft direction. The internal talonid rim appears to run to the metaconid without pronounced notch. Details are, however, obscured by the loss of the metaconid through breakage. The entoconid is not present as a distinct cusp, but is obscured by the curving posterior crest of the talonid. The protolophid is rather well developed, and in the existing stage of wear tends to form a pit-like enclosure.

No. 1794 does not agree in dentition with any of the Recent forms of ground-squirrel, but lack of adequate material makes comparison of little value. Absence of a distinct notch anterior to the entoconid, compression of the basin, and development of the protolophid may be characters tending to distinguish this form from related Recent ground-squirrels. Among Recent squirrels, however, the lack of a distinct notch is observed in some specimens of *Eutamias*, but other characters serve to distinguish the fossil from that genus.

*Otospermophilus gidleyi* from the Rattlesnake<sup>1</sup> may be distinguished by heavier jaw, slightly larger size, and possibly by a slightly less elevated posterior talonid rim than in No. 1794. Judging from the original description, the Rattlesnake species agrees with the Smiths Valley form in lack of a distinct internal notch in front of the entoconid, and in the relatively broad basins of the cheek-teeth. The species of *Citellus* from the Thousand Creek<sup>2</sup> does not have the comparable tooth present and the existing figure is not detailed enough for comparison. This specimen is smaller than No. 1794, but size difference is in part, at least, a function of position in the ramus.

Within the author's knowledge no fossil ground-squirrel known to occur earlier than those of the upper Pliocene or Pleistocene exhibits the typical ground-squirrel specializations in the dentition. Typical *Citellus* apparently does not arise until this stage of the Cenozoic.

<sup>1</sup> J. C. Merriam, C. Stock, and C. L. Moody, Carnegie Inst. Wash. Pub. No. 347, 68-69, figs. 23 a, b, 1925.

<sup>2</sup> Louise Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, No. 29, pp. 427-428, fig. 8, 1910.



## Measurements (in millimeters)

	No. 1795	No. 1794
P 4-M3, alveolar length.....	9.0 (a)	...
M2, antero-posterior diameter.....	...	2.1
M2, transverse diameter.....	...	2.5

(a) Approximate.

## GEOMYIDÆ

*Pliosacomys dubius*<sup>1</sup> n. gen. and sp.

*Holotype*—A right ramus with P4-M3, Calif. Inst. Tech. Coll. Vert. Pale., No. 1796 (Plate 2, figs. 2, 2a).

*Paratypes*—Fragmentary rostral portion of skull, Calif. Inst. Tech. Coll. Vert. Pale., No. 1797 (Plate 1, figs. 2, 2a). Palatal fragment bearing right P4-M2 and left P4-M1, Calif. Inst. Tech. Coll. Vert. Pale., No. 1798 (Plate 1, fig. 4).

*Referred Material*—A number of maxillary fragments and rami with teeth in varying stages of wear.

*Locality*—Smiths Valley, Lyon County, Nevada. Locality 174, C.I.T.

## GENERIC AND SPECIFIC CHARACTERS

Jaw heavy. Dentition in contrast slender and tooth-row short. P4/4 composed of a double column. P4 with posterior column forming a compressed ellipse in cross-section, anterior column becoming subcircular with wear; median union of anterior and posterior columns. Premolars not becoming similar to molars with wear, as in *Entoptychus* and *Pleurolicus*. Dentition hypsodont, apparently more so than in any known heteromyid from an horizon of similar age. Partial development of Y-pattern with subsequent formation of lakes in posterior and anterior lophs of upper and lower molars, respectively, at particular stage of wear.<sup>2</sup> Worn inferior molars almost rectangular, but slightly tapering toward lingual side. Enamel band on occlusal surface of teeth essentially continuous. Anterior faces of incisors flat and wide. Rostrum not arched. Palate sculptured. Zygomasseteric structure apparently as in Geomyidæ. Size approximately as in *Thomomys monticola mazama*; slightly larger than *Cupidinimus magnus* (Kellogg).

## DESCRIPTION

*Skull*—Available skull parts are limited to the palatal portion of the maxillaries and to a fragment of the rostral portion of a skull, No. 1797 (Plate 1, figs. 2, 2a). However, such portions of the skull as are in the collection furnish characters which indicate geomyid affinities for *Pliosacomys*. The rostral region is relatively heavy without arching of the inferior border of the rostrum. The latter, however, is a distinctly heteromyid rather than geomyid character. The skull is molded around the roots of the incisors for added strength as in Geomyidæ generally, contrasting in

<sup>1</sup> The generic designation is not intended to imply a reinstatement of the name *Sacomys* Cuvier (equals *Heteromys*), but is chosen with reference to the old name *Sacomys* Baird (equals *Geomyoidea*).

<sup>2</sup> A. E. Wood, Ann. Carnegie Mus., vol. 24, p. 168, 1935. "In the lower molars the . . . buccal movement of the protoconid toward the protostylid has made a deep fold between these two cusps, and caused a migration of the external cingulum to the anterior side of the tooth where it becomes an anterior cingulum. A result is to give the loph the shape of a Y, whence it is referred to as a Y-pattern."

this regard with the *Heteromyidæ*. The entrance to the infraorbital canal is protected from muscle pressure by countersinking in a sulcus. There is no evidence of a transverse canal extending through the rostrum. This last character appears to possess considerable importance in assigning *Pliosaccomys* to the *Geomyidæ*.

According to Miller and Gidley,<sup>1</sup> in Recent *Heteromyidæ* the "orifice of [the] infraorbital canal [is] protected from muscle pressure by countersinking in a vacuity which extends transversely through [the] rostrum." In the *Geomyidæ*, its orifice is "protected from muscle pressure by countersinking in an oblique sulcus." Presence of a vacuity in a skull of *Perognathoides quartus* (U.C. No. 29639) from the Fish Lake Valley lower Pliocene beds, and in a skull of *Perognathus furlongi* (C.I.T. No. 35) from the Cuyama Valley upper Miocene beds, demonstrates that this character was already established prior to the Smiths Valley stage. The incisive foramina are long and narrow, somewhat larger than those in either Recent *Thomomys* or *Heteromys*. The premaxillaries appear to be fused to a single bone as in Recent *Geomyidæ*. The premaxillary-maxillary suture is slightly in advance of the sulcus of the infraorbital canal and considerable unbroken bone is present posterior to the suture. In *Heteromys* the suture is just in advance of the infraorbital vacuity. For this reason a small area farther back in which bone is missing from the lateral wall of the maxillary can not be interpreted as a vacuity. Moreover, bone is present between this point and the entrance to the infraorbital canal proper. At the point where breaking away of the bone occurs, the maxillary in Recent *Geomyidæ* is very thin. A second specimen, which consists of a fragment of maxillary and premaxillary, does not show a very decided sulcus but neither does it possess apparently a transverse canal. So little of this specimen exists that the apparent shallowness of the sulcus may be due, at least in part, to its fragmentary character. An examination of this fragment tends to show that the incomplete character of the maxillary in No. 1797 is due to breakage.

The most superior point reached by the incisors in their backward course is somewhat below the dorsal surface of the skull. In *Heteromyidæ* the incisors reach almost the roof of the rostrum. The former condition apparently strengthens the skull against pressure exerted by the incisors. The narrow palate is rather heavily sculptured, much more so than in Recent *Heteromyidæ*, and approaches in this character those found in the *Geomyidæ*. Narrowness of palate is another point of resemblance to the *Geomyidæ*. The palate in the *Heteromyidæ* is relatively wider. From what remains of the incisors, it may be conjectured that they were somewhat protruding, but the premaxillaries and nasals may have projected anteriorly farther than in Recent gophers.

*Upper Dentition*—The upper incisors are relatively wide in section and but slightly rounded. No definite grooving of the incisors can be observed.

The fourth upper premolar is a persistently double-columned tooth. In the paratype, the anterior column (protoloph) is triangular in cross-section and is the smaller of the two columns. The posterior column (metaloph) is subcrescentic in outline and joins the protoloph toward the inner margin of the tooth. The tooth is divided into two columns by means of inner and outer re-entrant folds in the enamel. The inner fold is the more anterior and shallower of the two. No. 1800, a right maxillary with P4-M2 (Plate 1, fig. 3), possesses P4 in an unworn state. Details of construction are rather

<sup>1</sup>G. S. Miller and J. W. Gidley, Jour. Acad. Sci., vol. 7, No. 13, 433-434, 1918.



difficult to determine, but the protoloph may be composed of more than a single cusp. The metaloph is composed principally of two parts, the posterior portion is apparently made up of two cusps placed side by side (metacone and hypocone), which soon unite to form a single broad column. At the inner border and somewhat in advance of the metacone and hypocone is a crescentic cusp (entostyle) which connects the metaloph and protoloph. A cingular ridge forms the postero-internal border of the tooth, connecting with the entostyle in front and internally, and with the midpoint of the posterior border of the metacone-hypocone column behind. This pattern-stage prevails but a short time in the life of the individual. No. 1801, left maxillary with P<sub>4</sub>-M<sub>1</sub>, shows the occlusal pattern in old age in which the re-entrants are about equal in depth and are opposite each other. Both columns form compressed ellipses in cross-section with the metaloph the larger.

The type of P<sub>4</sub> present in Nos. 1800 and 1798 is superficially similar to that developed in *Liomys* and *Heteromys*, especially the latter. The chief points of difference, when *Pliosaccomys* is compared to *Heteromys*, is in the attachment, immediately upon wear, of the entostyle to the protoloph in the former as well as in the more angulate, less-rounded appearance of the entostyle. P<sub>4</sub> of *Pliosaccomys* exhibits strong resemblance to the comparable tooth in *Thomomys monticola* in the lingual attachment of the two columns and in the shape of the metaloph. Unfortunately, no unworn upper premolars of *Thomomys* are available for comparison.

No third molar is represented in the collection. The remaining two molars are so nearly alike, except that M<sub>1</sub> is slightly larger than M<sub>2</sub>, that the description of one will suffice. M<sub>1</sub> is bilophodont in early stages of wear, but is soon reduced to a single column by the union of the two lophs (metaloph and protoloph) at the lingual border. The intervening valley disappears and the occlusal pattern becomes rather rectangular with a re-entrant fold of more or less depth at the buccal border. In extreme wear the pattern is more elliptical, but the buccal inflection persists. No. 1800 possesses M<sub>1</sub> and M<sub>2</sub> in a relatively unworn state. In this specimen (Plate 1, fig. 3) it is seen that the anterior loph or protoloph, although rather compressed and linear, is made up of more than a single cusp. Judging from the faint swellings in the enamel, the protoloph may be composed of three distinct cusps as in the Geomyoidea generally. The posterior loph or metaloph is more crescentic and is rather similar to the posterior loph of the premolar. Two transversely placed cusps (metacone and hypocone) form the straighter portion of the metaloph. Posterior and median to these cusps a cingular ridge originates which forms the postero-internal border of the tooth. As this ridge curves forward it swells slightly into a cusp (entostyle), which with wear unites with the innermost of the three forward cusps, the protostyle. Moreover, the inner of the two posterior cusps (hypocone) also unites, with wear, to the more lingual part of the cingular ridge. Hence, the metaloph soon assumes a rather linear outline curving forward at its inner border to unite with the protoloph.

It should be mentioned that in the cheek-teeth, both upper and lower, the enamel forms a continuous band about the tooth. This is in decided contrast to Recent Geomyidæ in which the enamel is discontinuous and arranged in plates. Several rather worn specimens have minor interruptions of the enamel. These interruptions may have significance in indicating a trend toward the discontinuous plates of modern Geomyidæ, but



are too indefinite in character to have much weight attached to them in *Pliosacomys*.

Four maxillary specimens are present in the collection. It is with some doubt that they are assigned to a single species. No. 1799, a palatal fragment with left P<sub>4</sub>-M<sub>2</sub>, right P<sub>4</sub>-M<sub>1</sub> (Plate 1, fig. 8), differs from the paratype No. 1798 not only in smaller size but in character of tooth-pattern as well. However, the teeth are somewhat less worn and this fact may account for some of the apparent differences. If splitting of species were inaugurated on the basis of variation in tooth-pattern and rami of *Pliosacomys*, a number of species would have to be established within this genus. The entire rodent fauna described in the present paper was obtained from one exposure within a radius of 25 feet or less. It seems more reasonable to assume that all specimens of *Pliosacomys* represent a single species rather than that a number of closely allied species were preserved in this limited area.

*Ramus*—The ramus is relatively heavy and stout for the size of the dentition. The ridge for attachment of the masseter medialis muscle is short and generally not very well defined. The masseter lateralis ridge, however, is clearly indicated, at least as far back as the last molar. The ridge appears to be better developed than in *Heteromys*; less developed than in *Thomomys*. The ascending ramus has its origin opposite the penultimate molar. Valuable characters for distinguishing Recent Geomyidæ from Recent Heteromyidæ lie in the posterior portion of the ramus, notably in the character of the angle. Unfortunately, this region of the jaw is very imperfectly preserved in *Pliosacomys*, and little can be ascertained regarding its exact shape. The angle apparently was of more normal type than in Recent Geomyidæ, perhaps approaching that in *Entoptychus*. At any rate, it appears to have been more inferior in position than in Recent genera. The protuberance on the side of the ramus, marking the posterior termination of the incisor, was apparently extremely well developed, as in the Geomyidæ. This character is not especially noteworthy in the Heteromyidæ. Judging from the imperfectly preserved jaws, the plate of bone bearing the coronoid and condyle must have been rather high. Unfortunately, neither coronoid nor condyle is preserved in any of the specimens. The incisor terminates considerably in back of the dental foramen and somewhat above it.

*Lower Dentition*—The inferior incisor is relatively broad with flat anterior face. This character is seen in Recent gophers, but Recent pocket-mice have the enamel band rounded with the incisor as a whole more compressed. In *Dipodomys spectabilis* the anterior face of the lower incisor is flattened. However, it is not so flattened as in *Pliosacomys*, nor is the incisor relatively so broad.

As in the upper premolar, P<sub>4</sub> is persistently double-columned. The anterior column (protolophid) is sub-circular in cross-section. The posterior column (metalophid) is much compressed antero-posteriorly. The two lophs are joined at their mid-points, forming a modified X-pattern.<sup>1</sup> No. 1809, a left ramus with P<sub>4</sub>-M<sub>2</sub> (Plate 1, fig. 7), possesses an unworn fourth premolar. The metalophid appears to show traces of three cusps, metaconid, hypoconid, and an intermediate cusp. The protolophid is rather complex, but appears to be formed essentially of three cusps arranged in a trefoil. These cusps are apparently analogous, from lingual to buccal side,

<sup>1</sup> A. E. Wood, *op. cit.* 99, 1935.

to Wood's protoconid, anteroconid, and mesoconid.<sup>1</sup> The uneven surface of the unworn enamel indicates the presence of one or two anterior accessory cusps. With wear the trefoil runs together, becoming a simple, sub-circular column. One of the anterior re-entrant folds may persist for some time as a shallow inflection. The metalophid also possesses some irregularities in early stages of wear, but these do not persist for long. P $\bar{4}$  does not seem to be particularly close in pattern to any heteromyid, except in the worn state where all traces of original pattern are lost. It is not at all close to *Heteromys* or to any of the heteromyines.

The first two lower molars are mirror images of M $\bar{1}$  and M $\bar{2}$ , as is the case in so many rodents. However, since at least eight lower jaws of *Pliosacomys* are available, the change of occlusal pattern with wear is satisfactorily demonstrated. The teeth are bilophodont in the younger stages of wear, becoming monolophodont with age. The posterior loph (hypolophid) is narrow and linear. The number of cusps composing it can not be definitely determined, but there is some indication of a normal three-cusped loph (entoconid, hypoconid and hypostylid). The anterior loph (metalophid) is composed of two cusps, the metaconid and protoconid, with a cingular ridge originating in front and at the lingual side of the protoconid, forming the antero-external portion of the tooth (thus forming a partial Y-pattern). This ridge terminates in a small cusp, the protostylid. The valley intervening between the cingular ridge and the metalophid is rather shallow so that with wear the whole front half of the tooth soon unites to form a wedge-shaped loph with the point directed toward the lingual border. For a greater or less time the remnants of the intervening valley persist as an enamel islet. The valley between metalophid and hypolophid is shallow, so that with continued wear the two lophs unite at the buccal border. The occlusal pattern is then somewhat rectangular in section with an inflection of more or less depth on the lingual side. In old age all inflections disappear.

The third lower molar differs somewhat from the remaining two in possessing a more circular outline. It may also differ in that the external portion of the valley between the two lophs tends to remain as a re-entrant fold in the enamel, thus forming with the lingual fold the H-pattern described by Wood.<sup>2</sup>

The lower deciduous premolar is represented in the collection by No. 1810 (Plate 1, fig. 1), a fragment of jaw bearing this tooth. The tooth is brachydont and extended antero-posteriorly. It is apparently composed of an internal and external row of low cusps, four on a side, all more or less connected. A second jaw in the collection also bears this tooth in a worn state. Fortunately, all three permanent molars are present, so that no doubt exists in referring No. 1810 to *Pliosacomys*.

#### COMPARISONS

If *Pliosacomys* is to be assigned to the Geomyidæ, the dentition shows a striking amount of parallelism to the Heteromyidæ. A. E. Wood has recently published a careful and complete account of the evolution and relationships of the heteromyids.<sup>3</sup> In this publication, Wood has divided the group, following an earlier classification of Coues, into three subfamilies, namely Perognathinæ, Dipodomyinæ, and Heteromyinæ. Comparisons with

<sup>1</sup> A. E. Wood, *op. cit.* 79, fig. 1a, 1935.

<sup>2</sup> A. E. Wood, *op. cit.* 101, 1935.

<sup>3</sup> A. E. Wood, *op. cit.* 1935.



these subfamilies show that although *Pliosacomys* may resemble the members of a particular line in some respects, it disagrees quite radically in others. The following selected differences distinguish *Pliosacomys* from members of the various heteromyid subfamilies as these groups are defined by Wood.

*Distinguished from Perognathinae by:* Lophs of P<sub>4</sub> unite at lingual border; development of lakes in molars result from partial development of a Y-pattern in posterior and anterior lophs of upper and lower molars respectively; P<sub>4</sub> with more than four cusps; no development of H-pattern, with possible exception of M<sub>3</sub>, contrasting with progressive members of the Perognathinae.

*Distinguished from Dipodomysinae by:* Lophs of P<sub>4</sub> unite at lingual border; partial development of Y-pattern in molars with subsequent formation of lakes; P<sub>4</sub> apparently more than five-cusped; H-pattern not developed in lower molars except possibly in M<sub>3</sub>; pattern of cheek-teeth apparently somewhat more deeply impressed on tooth-crown.

*Distinguished from Heteromyinae by:* Lophs of P<sub>4</sub> never unite at buccal side; P<sub>4</sub> with modified X-pattern (at least protolophid unites with median portion of metalophid).

Characters in the skull and ramus of *Pliosacomys* already discussed, appear to distinguish the genus from the Heteromyidae as a whole.

One species of heteromyid, *Cupidinimus magnus* (Kellogg) (equals *Diprionomys magnus* Kellogg)<sup>1</sup> is rather close to the Smiths Valley form. *Cupidinimus magnus* is based on two specimens, established as type and cotype by Louise Kellogg. The type, U.C. No. 12567 is a lower jaw with P<sub>4</sub>-M<sub>2</sub>. M<sub>2</sub> in No. 12567 is definitely wider than M<sub>1</sub>. In *Pliosacomys*: M<sub>1</sub> and M<sub>2</sub> are subequal in width. Other differences are, in *Pliosacomys*: the lateral folds of M<sub>1</sub> and M<sub>2</sub> do not extend downward as far as in No. 12567; mental foramen larger and more superior in position; ramus may be relatively more heavy; and masseter muscle scar probably better defined and less horizontal. The cotype of *C. magnus*, U.C. No. 12568, is a fragment of ramus with P<sub>4</sub>. It shows the same general type of premolar construction that occurs in *Pliosacomys*, the incisor has a flat anterior face (relatively rare in heteromyids) and the masseter muscle scar is of the same type of construction as in our genus. The Smiths Valley genus differs in perhaps slightly larger size than No. 12568; mental foramen probably somewhat more superior in position; and perhaps in somewhat different pattern of P<sub>4</sub>. With regard to this last character, *Pliosacomys* seems to possess a slightly more complicated pattern at the same stage of wear, although a more worn specimen of the genus may be quite similar. Nos. 12567 and 12568 presumably represent the same species, although because of the fragmentary nature of the material this can not be absolutely demonstrated. If the two are to be assigned to a single species, they differ from *Pliosacomys* chiefly in the molar teeth, as outlined above. A specimen from San Pedro Valley, referred by Wood to *C. magnus*, consisting of P<sub>4</sub>-M<sub>1</sub> with associated upper incisors, is clearly not related to our genus.<sup>2</sup> It is possible that apparent similarity of the cotype of *Cupidinimus magnus* to *Pliosacomys* results largely from the incompleteness of the former specimen.

Comparison of *Pliosacomys* with fossil types known to be related to the geomyids is limited by lack of material. This dearth or absence of material is especially noteworthy for that long period of time which inter-

<sup>1</sup> Louise Kellogg, Univ. Calif. Pub., Bull. Dept. Geol., vol. 5, No. 29, 434-435, fig. 18, 1910.

<sup>2</sup> A. E. Wood, *op. cit.* 146-148, 1935.



vened between the lower Miocene and upper Pliocene. The earliest forms which have been referred to the Geomyidæ are *Entoptychus* and *Pleurolicus* from the John Day and related formations. These genera have been grouped by Miller and Gidley as a subfamily, Entoptychinæ, of the Geomyidæ.<sup>1</sup> Limited comparative material at hand makes many comparisons difficult or impractical. *Entoptychus* is an extremely specialized genus for this stage in the history of the gophers. It is distinguished from *Pliosacomys* by many characters in the skull, rami and dentition, as well as by a wide separation in time. Selected differences are as follows: In *Entoptychus* (1) cheek-teeth with persistent? growth, (2) P4/4 assume a molar-pattern on wear, (3) cheek-teeth tend to form lakes between lophs, and (4) inferior border of rostrum arched. *Pleurolicus*, judging from the description of the genus by Cope<sup>2</sup> and by Matthew,<sup>3</sup> is similar to *Entoptychus*, except that the former possesses rooted cheek-teeth. As in *Entoptychus*, the premolars of *Pleurolicus* wear to a pattern much like that of the molars. In view of the fundamental difference in premolar pattern and the early specialization of *Entoptychus*, the group does not seem to be related to either the Smiths Valley genus or to other known Geomyinæ. The upper Pliocene and Pleistocene gophers all differ widely from *Pliosacomys* in the differentiation of the enamel of the cheek-teeth into discontinuous bands, the persistent growth of the cheek-teeth, and in many other characters as well. A few specimens are known from the middle and later Tertiary and have been referred to Recent genera. These forms presumably differ widely from *Pliosacomys*.

#### RELATIONSHIPS

Virtually all workers stress the close connection between the Heteromyidæ and the Geomyidæ. As a matter of fact, many of the striking differences between the two families are traceable directly to differences in habits of life. The Smiths Valley specimens confirm this view and, indeed, very strongly suggest not only a close relationship, but also a descent of the gophers from the pocket-mice, or at least a descent from a common ancestor whose resemblance to pocket-mice would be indicated by an absence of fossorial characters as well as by tooth pattern. This corresponds to a view expressed many years ago by W. B. Scott.<sup>4</sup>

The exact relationships of *Pliosacomys* are rather puzzling. In many of its characters the genus stands structurally between the Heteromyidæ and the Recent Geomyidæ. However, its late appearance in the fossil record indicates that probably it should be considered as only a persistently primitive and aberrant geomyid, but exhibiting perhaps a stage similar to that passed through by the main line of the gophers (Geomyinæ) in their evolution toward Recent types.

A. E. Wood has shown that the Heteromyinæ and the Perognathinæ (plus Dipodomynæ) were apparently distinct by lower Miocene (Harrison) time. The evidence, however, is based on relatively poor material. Since *Pliosacomys* combines characters of both groups, the line it represents presumably would also have been distinct by that time. At any rate, the presence of the Entoptychinæ in the John Day and Harrison stages shows that this branch of the Geomyidæ was differentiated. The middle Oligocene rodent *Heliscomys* is regarded by Wood as the "starting point for the

<sup>1</sup> G. S. Miller and J. W. Gidley, Jour. Wash. Acad. Sci., vol. 8, No. 13, 433-434, 1918.

<sup>2</sup> E. D. Cope, Report U. S. Geol. Surv. Terr., vol. 3, Bk. 1, 866-867, 1884.

<sup>3</sup> W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 23, Art. 9, 211-212, 1907.

<sup>4</sup> W. B. Scott, Proc. Acad. Nat. Sci. Phila., 284, 1895.

evolution of the later Heteromyidæ." He states: "It is possible that *Heliscomys* is the common ancestor of the Heteromyidæ and Geomyidæ, but the gap between it and the earliest geomyids is so great and the time so short as to make this virtually impossible. It is almost certain, however, that *Heliscomys*, as far as dental development is concerned, is structurally ancestral to the geomyids."<sup>1</sup> There is certainly no character in *Pliosacomys* which would suggest that this genus and the Geomyinæ were differentiated from the heteromyids before the middle Oligocene. If anything, the genus suggests by the parallelism displayed in the cheek-dentition a somewhat later separation. It is possible that the Entoptychinæ, in view of the precocious specialization along certain lines in *Entoptychus*, represents the first branching-off of the gophers from the central stock and the Geomyinæ a somewhat later one. No unworn teeth of *Entoptychus* are available for comparison, so that the degree of relationship of this form to the early heteromyids, *Pliosacomys*, or to other geomyids, as evidenced by dental structure, could not be investigated.

Records of Geomyinæ before the upper Pliocene are extremely rare. W. D. Matthew mentions the presence of *Thomomys* in the Deep River and Nebraska Miocene stages in a chart accompanying his paper on the affinities of the Ischyromyidæ.<sup>2</sup> I am not familiar with any papers by Matthew or by other authors containing more specific statements concerning these forms. H. J. Cook and M. C. Cook, in a paper entitled "Faunal Lists of the Tertiary Vertebrata of Nebraska and Adjacent Areas,"<sup>3</sup> list *Thomomys* species as coming from the lower Snake Creek. A record of an existing genus in a stage as early as the Deep River is very unusual. If these determinations prove correct, *Pliosacomys* has little to do with the main line of the Geomyidæ. Marsh established a new species, *Geomys bisulcatus*,<sup>4</sup> for a specimen from "Pliocene strata, near Camp Thomas, on the Loup Fork river." The incisors are double-grooved and the molars are close to those in *Geomys bursarius*. H. J. Cook and M. C. Cook, in their paper cited above, list *G. bisulcatus* as questionably present in the Fort Niobrara (upper Miocene) and the lower Snake Creek. From the Snake Creek Pliocene, Matthew describes a rodent jaw, without teeth, which he first referred to *Geomys*<sup>5</sup> and later apparently to *Thomomys*.<sup>6</sup> H. J. Cook and M. C. Cook list both genera as occurring in the upper Snake Creek fauna. The Pliocene records are not so confusing as the Miocene occurrences, but confirm the view that *Pliosacomys* is not the lineal ancestor of any of the modern gophers. As stated previously, the upper Pliocene and Pleistocene geomyids are clearly advanced types, closely related to Recent forms and not closely allied to the Smiths Valley genus.

The history of the Geomyidæ, taking the earlier identifications and assignments at their maximum worth, a gratuitous assumption at best, might seem to cast doubt on the recognition of *Pliosacomys* as a geomyid. A possible alternative explanation of the relationships of *Pliosacomys* lies in the view that this genus is a heteromyid with geomyid specializations. However, this view does not have much in its favor. As mentioned previously, if the Heteromyinæ and Perognathinæ (plus Dipodomyinæ) were separate as far back as the lower Miocene, then the line of development

<sup>1</sup> A. E. Wood, *op. cit.* 82-83, 1935.

<sup>2</sup> W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 28, Art. 6, 67, fig. 19, 1910.

<sup>3</sup> H. J. Cook and M. C. Cook, Nebr. Geol. Surv., Paper No. 5, 49, 1933.

<sup>4</sup> O. C. Marsh, Amer. Jour. Sci., Third Ser., vol. 2, Art. 17, 121-122, 1871.

<sup>5</sup> W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 26, Art. 27, 382-383, 1909.

<sup>6</sup> *Loc. cit.*, vol. 50, Art. 2, 68, 1924.



represented by *Pliosacomys* was without much doubt also distinct at that time. Moreover, unless the perforate character of the rostrum is acquired more than once, this feature during the lower Miocene was present in all heteromyids which eventually gave rise to Recent types. Indeed, it is safe to say that the common ancestor of all the recognized heteromyid groups must also have possessed this character. The *Pliosacomys* line, on the other hand, is distinguished by an imperforate rostrum and the source of the several phyletic developments would consequently be still further removed in time, namely, to a position not very remote from that occupied by the common ancestor for both the Geomyidæ and Heteromyidæ. In other words, the *Pliosacomys* line becomes geomyid virtually by definition. It must be admitted that the above reasoning is tenuous, but is perhaps as justifiable as an alternative explanation. As a matter of fact, the dental characters of *Pliosacomys* which sometimes parallel those of one, sometimes those of another, of the heteromyid subfamilies are themselves in favor of geomyid affinities. Direct evidence is seen in the definite geomyid characters of skull and jaws, already discussed, with perhaps the chief negative or heteromyid character presented by the unarched rostrum.

A careful review of all fossil geomyid material would undoubtedly shed light on the evolution of the gophers. At present even figures of late Miocene and early Pliocene Geomyinæ are not available.

A little additional evidence, which throws some light on the characters in the cheek-dentition of *Pliosacomys*, is furnished by the unworn teeth of Recent gophers. C. Hart Merriam figured the relatively unworn teeth of *Geomys*. A figure of a ramus of this genus<sup>1</sup> with relatively unworn cheek-teeth shows that in the unworn state, and for a short time after wear has started, the enamel continuously surrounds the dentine. An M $\bar{1}$  and M $\bar{2}$  also show patterns not unlike those developed in *Pliosacomys*. M $\bar{2}$ , in which the tooth is still divided into two lophs, possesses a metalophid which is wedge-shaped, and a narrow hypolophid, very much like that in the corresponding tooth in *Pliosacomys*. Another figure of Merriam's, that of *Heterogeomys*,<sup>2</sup> shows a decided H-pattern in the lower molars, a characteristic not of *Pliosacomys*, but of the Dipodomysinæ. A milk molar of *Geomys*,<sup>3</sup> although badly worn, resembles *Pliosacomys* in relatively great antero-posterior diameter, but this is a character common to both heteromyid and geomyid milk teeth. An unworn P $\bar{4}$  of *Thomomys* from the Carpinteria asphalt deposits of upper Pleistocene age, although apparently differing in several points, is as much like the unworn P $\bar{4}$  of *Pliosacomys*, as that tooth in the latter genus is like any known heteromyid premolar.

#### CONCLUSIONS

*Pliosacomys* is best assigned to the family Geomyidæ and subfamily Geomyinæ. Many of its characters indicate the close relationship of the Geomyidæ to the Heteromyidæ. The genus can not be directly ancestral to any existing gopher, but, in cheek-tooth characters at least, may show a structural stage through which the Geomyinæ have passed.

<sup>1</sup> C. H. Merriam, U. S. Dept. Agric., North Amer. Fauna, No. 8, 252, pl. 16, fig. 4, 1895.

<sup>2</sup> C. H. Merriam, *op. cit.* 252, pl. 16, fig. 2, 1895.

<sup>3</sup> *Op. cit.* 252, pl. 16, fig. 2, 1895.



## Measurements (in millimeters)

	<i>Pliosaccomys dubius</i>	
	No. 1794	No. 1798
Length of diastema between $\bar{I}$ and $P_4$ .....	10.6	...
Width of palate between $P_4$ .....	...	2.3
$\bar{I}$ , antero-posterior diameter.....	1.8	...
$\bar{I}$ , transverse diameter.....	1.9	...
Alveolar length, $P_4$ - $M_2$ , inclusive.....	...	5.0 (a)
$P_4$ , antero-posterior diameter (occlusal surface).....	...	1.7
$P_4$ , transverse diameter.....	...	1.8
$M_1$ , antero-posterior diameter.....	...	1.1
$M_1$ , transverse diameter.....	...	1.7
$M_2$ , antero-posterior diameter.....	...	1.0
$M_2$ , transverse diameter.....	...	1.7
(a) equals approximate.		
	No. 1796	
Depth of jaw below $P_4$ .....	5.1	
Alveolar length $P_4$ - $M_3$ , inclusive.....	6.1	
$P_4$ , antero-posterior diameter (occlusal surface).....	1.3	
$P_4$ , transverse diameter.....	1.3	
$M_1$ , antero-posterior diameter.....	1.2	
$M_1$ , transverse diameter.....	1.6	
$M_2$ , antero-posterior diameter.....	1.1	
$M_2$ , transverse diameter.....	1.7	
$M_3$ , antero-posterior diameter.....	1.1	
$M_3$ , transverse diameter.....	1.5	
$\bar{I}$ , antero-posterior diameter (average of three specimens).....	1.6	
$\bar{I}$ , transverse diameter (average of three specimens).....	1.4	
Alveolar length $P_4$ - $M_3$ inclusive (average of four specimens).....	5.8	

## ZAPODIDÆ

*Pliozapus solus* n. gen. and sp.

*Genotype*—A right ramus with  $M_1$ - $M_3$ , Calif. Inst. Tech. Coll. Vert. Pale., No. 1811 (Plate 2, figs. 4, 4a).

*Locality*—Smiths Valley, Nevada. Locality 174, C.I.T.

## GENERIC AND SPECIFIC CHARACTERS

$\bar{I}$ ,  $\bar{O}$ ,  $\bar{O}$ ,  $\bar{3}$ . Molar teeth broad, crowns brachydont? Enamel folds not crowded. Anteroconid absent in  $M_1$ . Rudimentary protolophid in  $M_2$ . Protoconid and hypoconid rounded, not angulate as in Recent Zapodinae. Metalophid gives off spur which encloses a small lake. Protoconid in  $M_1$  unites with protoconid-hypoconid ridge with moderate wear. Protoconid-hypoconid ridge relatively more antero-posterior in position than in Recent genera of Zapodinae. Angle of ramus much as in *Zapus*, condylar notch high. Size about as in *Zapus hudsonius*, but cheek-teeth relatively heavier.

## DESCRIPTION

The ramus of *Pliozapus* (Plate 2, fig. 4) is similar to that in Recent *Zapus* in general proportions, in so far as these may be judged from the imperfect specimen at hand. The important posterior region of the jaw is sufficiently preserved to show that the angle is essentially as in *Zapus*.

The jaw is readily distinguished from cricetine forms by the character of the angle which is a broad flattened plate, much inflected, its inferior border sharply keeled by the presence of the masseter lateralis ridge. The latter is strong and continuous from the angle up to and on the side of the ramus,

giving almost an hystricine appearance to the jaw. The ramus further differs from that of cricetine forms by possessing a notch between angle and condyle, which is U-shaped and superior in position.

The masseter muscle scar terminates about opposite the mid-point of M1. The fragmentary nature of the jaw makes it impossible to determine the presence or absence of a foramen between M3 and the ascending ramus. Such a foramen is not present in *Zapus* but is, in some members at least, of the *Sicistinae*.

The compressed incisor has a convex anterior face. It is not noticeably different in character or in point of origin from that in *Zapus*.

The cheek-teeth, three in number, are relatively broad with brachydont? crowns. The exact height of crown is difficult to ascertain. The fact that the cheek-teeth are, in their present stage of wear, very short-crowned and the pattern is still rather clear points toward a rather brachydont type. M1 and M3 are three-rooted, the intermediate molar is four-rooted.

The grinding teeth (Plate 2, fig. 4a) are rather worn, so that details of tooth-pattern are in certain instances somewhat obscured. M2 is relatively broad for a zapodid tooth, in general proportions it is somewhat like the corresponding tooth in *Sicista*. It is, however, longer than wide. The tooth-crown is essentially quadritubercular. The two inner cusps are smaller but apparently higher than the outer pair. Moreover, the inner cusps, set somewhat in advance of the outer, are compressed into lophs and the inner cusps themselves are obscured. These four cusps apparently represent the protoconid, metaconid, hypoconid, and entoconid. A small cusp is situated in front of the protoconid and metaconid and somewhat toward the external margin of the tooth. This cusp corresponds in position to the paraconid of other orders, but the paraconid is usually lost in rodents. Its place is sometimes taken by a cingular cusp. Schaub, in his work on the fossil *Sicistinae*, has referred to this cusp as a paraconid.<sup>1</sup> In the present paper Wood's term, anteroconid,<sup>2</sup> will be used. The metaconid, protoconid, and anteroconid are united by a transverse loph, in the present case at least, best termed the metalophid. The hypoconid is worn into a large flat cusp, with a strong hypoconulid ridge forming the posterior margin of the tooth. The protoconid and hypoconid are united by an antero-posterior and somewhat oblique ridge, the protoconid-hypoconid ridge. A small metastylid just posterior to the metaconid is compressed into an oblique loph which joins externally with the protoconid-hypoconid ridge. Apparently, a short protolophid is present as a small spur given off internally from the protoconid. Moreover, the metalophid also gives off a spur, which projects posteriorly to join the metastylid loph and encloses a small crescentic lake. The entoconid is united to the posterior portion of the protoconid-hypoconid ridge by a strong entolophid, which more or less obscures the cusped nature of the entoconid.

The first molar is so worn that for the most part the original lophs and intervening valleys are confluent. The tooth narrows somewhat toward its anterior end. M1 lacks an anteroconid, and apparently this feature is not due to wear. The valley between metaconid and metastylid is reduced to a tiny notch. However, a small lake occupies a position similar to that in M2. The pattern of the posterior half of the tooth is obscured by breakage as well as by wear. A small median lake apparently represents the remnant of the valley between entolophid and hypoconulid ridge.

<sup>1</sup> S. Schaub, *Eclogæ geol. Helvetiæ*, 23, p. 622, 1930.

<sup>2</sup> A. E. Wood, *op. cit.* 79, fig. 1a, 1935.



M $\bar{3}$  is considerably reduced with regard to length. The anteroconid, if originally present, has been obliterated by wear. A lake corresponding to the lake in M $\bar{2}$  is present, as well as a second, antero-internal one which apparently represents the fusion of the metalophid and anterior cingulum. A point of difference between the last molar and the anterior two is seen in the metastylid which joins with the entoconid, and, moreover, lacks the oblique loph which in M $\bar{1}$  and M $\bar{2}$  joins this cuspule with the protoconid-hypoconid ridge. This character may be due to individual variation for in a mandible of *Eozapus*, available for comparison, the metastylid loph appears to be present on one side and absent on the other.

#### COMPARISONS AND RELATIONSHIPS

It seems clear that *Pliozapus solus* should be placed in the Zapodidae as that family is defined by Miller and Gidley. The Zapodidae, according to those authors, includes three subfamilies, namely, the extinct European Theridomyinae, the Eurasiatic Sicistinae, and the Asiatic and North American Zapodinae.<sup>1</sup> The various views of authors on the systematic position of the theridomyids do not concern us in the present paper, since *Pliozapus* clearly does not belong in this group. The Theridomyinae have large functional fourth premolars, became extinct in the Miocene, and are limited apparently in their distribution to the Old World. It is also clear that *Pliozapus* is much closer to at least some members of the Zapodinae than to the Sicistinae, and should be placed in the former subfamily.

North American fossil Dipodoidea, other than Pleistocene types, are limited to the Uinta *Protoptychus*<sup>2</sup> and to the John Day *Paciculus*.<sup>3</sup> Very little is known about the systematic position of either of these two genera. *Protoptychus* has been referred to the Dipodidae by Miller and Gidley, but these authors note the possible reference of this type to the Theridomyinae. A. E. Wood has suggested that the genus may represent an "aberrant and sterile offshoot of the Ischyromidae."<sup>4</sup> The only known specimen is a skull, so that comparisons with *Pliozapus* can not be made, except that, as inferred from the upper dental series, a functional P $\bar{4}$  must have been present. It may be presumed from the characters displayed by the upper dentition that the lower dentition was quite unlike that in *Pliozapus*. The John Day *Paciculus* has been placed in the Dipodidae by Hay.<sup>5</sup> Cope's figures of the lower jaws are not good enough to permit many general comparisons and no detailed ones.<sup>6</sup> *Paciculus* is much larger than the form from Smiths Valley and the proportions of the teeth are different. Judging from the fact that P $\bar{4}$  has already disappeared, *Paciculus* was probably an early specialization, certainly not closely related to the later zapodids.

*Sicista*, *Eozapus*, *Zapus* and *Napæozapus* comprise the Recent genera of the Zapodidae. The first belongs to the subfamily Sicistinae, the last three to the Zapodinae. Although the rami of *Zapus* and *Pliozapus* agree rather closely, so far as known, the cheek-dentition of the North American Recent zapodids, *Napæozapus* and *Zapus* are in sharp contrast to that of the Tertiary form. *Pliozapus* has broader, more brachydont teeth with decidedly less-modified patterns and broader reentrant folds. As a matter of fact, the cusps have been so completely converted into folds in the

<sup>1</sup> G. S. Miller and J. W. Gidley, *op. cit.* 422-443, 1918.

<sup>2</sup> W. B. Scott, *op. cit.* 269-286, 1895.

<sup>3</sup> E. D. Cope, Proc. Amer. Philos. Soc., 18, 370, 1879 (1880).

<sup>4</sup> A. E. Wood, *op. cit.* 239, 1935.

<sup>5</sup> O. P. Hay, Carnegie Inst. Wash. Pub. No. 390, vol. 2, 911, 1930.

<sup>6</sup> E. D. Cope, *op. cit.* pl. 66, fig. 32, 1884.



former genera that their differentiation would be extremely difficult to interpret were it not for the comparisons made available by *Pliozapus*. Using the terminology employed in the description of *Pliozapus*, the following additional differences among others may be mentioned: (1) protoconid-hypoconid ridge not present in *Zapus*, except when a connection is formed through wear, (2) entoconid and protoconid connected directly by a long crest in *Zapus*, in *Pliozapus* the two are not connected except by means of protoconid-hypoconid ridge, (3) anterior portion of  $M\bar{2}$  in *Zapus* disconnected from protoconid and metaconid in early stages of wear, and (4) hypoconulid ridge apparently double in *Zapus*.

The enamel pattern of *Napæozapus* is essentially similar to that in *Zapus*, but  $P_4$  is missing and there are minor differences as well.

Recent *Eozapus* from China is much closer to *Pliozapus* than is either of the two North American genera. It differs from the latter and agrees with the former (A) in not having the enamel folds crowded, (B) in possessing a protoconid-hypoconid ridge, (C) protoconid and entoconid connected only by means of this ridge, (D) anterior portion of  $M\bar{2}$  connected with posterior portion, and (E) in presence of a single hypoconulid ridge. *Pliozapus* differs from *Eozapus* in (A) presence of broader cheek-teeth, (B) presence of spurs on lophs which tend to enclose enamel lakes, (C) principal outer cusps less angulate, (D) probable less height of crown, (E) a short protolophid in  $M\bar{2}$ , (F) the metastylid loph of  $M\bar{2}$  slants forward instead of being transverse or sloping slightly backward, (G) protoconid-hypoconid ridge of  $M\bar{1}$  more antero-posterior, and lastly (H) in a possible better connection between trigonid and talonid in  $M\bar{1}$ .

The Recent Eurasiatic sicistid, *Sicista*, also makes a closer approach to *Pliozapus*, with regard to dental pattern, than do *Zapus* and *Napæozapus*. *Pliozapus* is distinguished from *Sicista* by: more oblique direction of protoconid-hypoconid ridge, anterior termination of this ridge at buccal portion of protoconid rather than between protoconid and metaconid as in *Sicista*; cusps more compressed into lophs; cheek-teeth somewhat broader; greater development of metastylid; greater development of hypoconulid ridge; protoconid and metaconid of  $M\bar{1}$  are more nearly opposed; absence of anteroconid in  $M\bar{1}$ ; angle a larger plate with condylar notch higher; and masseter lateralis ridge much better developed.

*Plesiosminthus* and *Heterosminthus*, fossil sicistids from the European Oligocene and the Asiatic Pontian, respectively,<sup>1</sup> possess the anteroconid in  $M\bar{1}$  weakly developed, and in this respect come closer to *Pliozapus* than does *Sicista*. However, *Heterosminthus* is quite unlike the North American genus in greater reduction, in the former, of the elements of  $M\bar{3}$ , combined with a much less advanced  $M\bar{1}$  and  $M\bar{2}$ . *Plesiosminthus* may be a more suitable ancestor for *Pliozapus* than *Heterosminthus*, but the wide geologic separation, lack of comparative material, and incomplete *Pliozapus* remains make comparisons of little value. It is sufficient to state that the two are generically quite distinct.

*Pliozapus solus* clearly falls into the Zapodinae. The genus stands, in a sense, ancestral to the structurally progressive series *Eozapus*, *Zapus*, and *Napæozapus*. Actually, *P. solus* can not be ancestral to *Eozapus* since it appears to have certain features, as for example the development of spurs on certain of the lophs, that are probably progressive characters. However, *Pliozapus* is closer to *Eozapus* than to any other genus, either living or extinct. This relationship demonstrates again the close connection between

<sup>1</sup> S. Schaub, *op. cit.* 1930.

certain Asiatic and New World groups of mammals from Pliocene time onward. If speculation may be permitted, it seems most likely that North America, in view of the relations of *Pliozapus* to existing genera, was the seat of evolution of the Zapodinae. The ancestry of *Pliozapus solus* must, for the present, remain in doubt.

*Comparative measurements (in millimeters)*

	<i>Pliozapus solus</i> No. 1811 C.I.T. Smiths Valley	<i>Eozapus s. vicinus</i> Smithsonian No. 240762 Recent China	<i>Sicista flava</i> Smithsonian No. 173808 Recent Kashmir	<i>Zapus h. hudsonius</i> Dickey Coll. No. 17078 Recent Ont- ario, Canada
Length of M1-M3 inclusive.....	3.9	3.5	3.1	3.4
M1, antero-posterior diameter.....	1.4	1.3	1.2	1.4
M1, transverse diameter.....	1.1	.9	.8	.7
M2, antero-posterior diameter.....	1.4	1.3	1.1	1.3
M2, transverse diameter.....	1.2	1.0	.9	.9
M3, antero-posterior diameter.....	1.1	1.0	.9	.7
M3, transverse diameter.....	1.0	.8	.7	.6

## CRICETIDAE

### *Peromyscus near antiquus* Kellogg

A left ramus with M1-M3, Calif. Inst. Tech. Coll. Vert. Pale., No. 1812 (Plate 2, figs. 3, 3a), of a cricetid rodent is very close to the Thousand Creek species, *Peromyscus antiquus*.<sup>1</sup> The dentition of the Smiths Valley form has the same proportions and length of tooth-row, but is somewhat less worn. M1 and M2 of No. 1812 are so close to the comparable teeth of the type of *P. antiquus* that difference in wear would account for any dissimilarities. However, the posterior cusp of M3 (hypoconid plus entoconid) is more compressed in an oblique direction than in *P. antiquus*. Moreover, the internal valley in the latter tooth is somewhat dammed at its mouth in the type, and this is not the case in No. 1812. These last two characters may not be due entirely to wear or individual variation. The ramus of No. 1812 seems deeper and heavier than that of *P. antiquus*, but the incomplete inferior border of the ramus in the type specimen possibly accounts for some of this difference.

Other species of *Peromyscus* appear to be quite distinct from the Smiths Valley form. *P. brachygnathus*, *P. minimus* and *Eligmodontia arizonæ* from the San Pedro Valley beds, Arizona,<sup>2</sup> are all much smaller than *P. near antiquus*, and have a more reduced M3. *P. dentalis* (Fish Lake Valley beds) and *P. longidens* (Barstow beds) are smaller and have less hypsodont teeth.<sup>3</sup> The various specimens referred to existing species or closely related forms are smaller than *P. near antiquus*, and tend to have more reduced third molars. Lastly, *P. loxodon* from the upper Miocene of New Mexico<sup>4</sup> is somewhat smaller. Apparently from Cope's description it differs also in having the molars more nearly subequal and shorter crowned.

<sup>1</sup> Louise Kellogg, *op. cit.* 432-433, fig. 16, 1910.

<sup>2</sup> J. W. Gidley, U. S. Geol. Surv., Prof. Paper 131, 124-125, 1922.

<sup>3</sup> E. R. Hall, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 19, Nos. 12, 13, 306-307, figs. 15-17, and page 315, figs. 5-7, 1930.

<sup>4</sup> E. D. Cope, U. S. Geol. Surv., West 110th Mer., vol. 4, 300-301, pl. 69, fig. 15, 1877.

The reference of the Smiths Valley form to *Peromyscus* follows the procedure adopted by various authors in describing extinct species of *Peromyscus*. If it were practical to employ, in dealing with fossil forms, the fine distinctions made in splitting Recent North American ericetids, several distinct genera doubtless would be established.

*Measurements (in millimeters)*

	<i>Peromyscus near antiquus</i>
	C.I.T. No. 1812
	Smiths Valley
Depth of ramus below M $\bar{1}$ .....	4.1
Length of M $\bar{1}$ -M $\bar{3}$ inclusive.....	5.6
M $\bar{1}$ , antero-posterior diameter.....	2.1
M $\bar{1}$ , transverse diameter.....	1.3
M $\bar{2}$ , antero-posterior diameter.....	1.8
M $\bar{2}$ , transverse diameter.....	1.4
M $\bar{3}$ , antero-posterior diameter.....	1.6
M $\bar{3}$ , transverse diameter.....	1.2

## LAGOMORPHA

### Leporid species

A single left lower grinding tooth indicates the presence of a leporid. The tooth is smaller than comparable topotype material of *Hypolagus vetus* (Kellogg). However, the specimen agrees rather closely in size with Pliocene remains obtained near Rome, Oregon, tentatively determined as representing *Hypolagus*. Characters other than size would be difficult to establish in the present instance. Several skeletal elements in the Smiths Valley collection also represent the Leporidæ.

*Measurements (in millimeters)*

Antero-posterior diameter.....	2.5
Transverse diameter.....	2.5



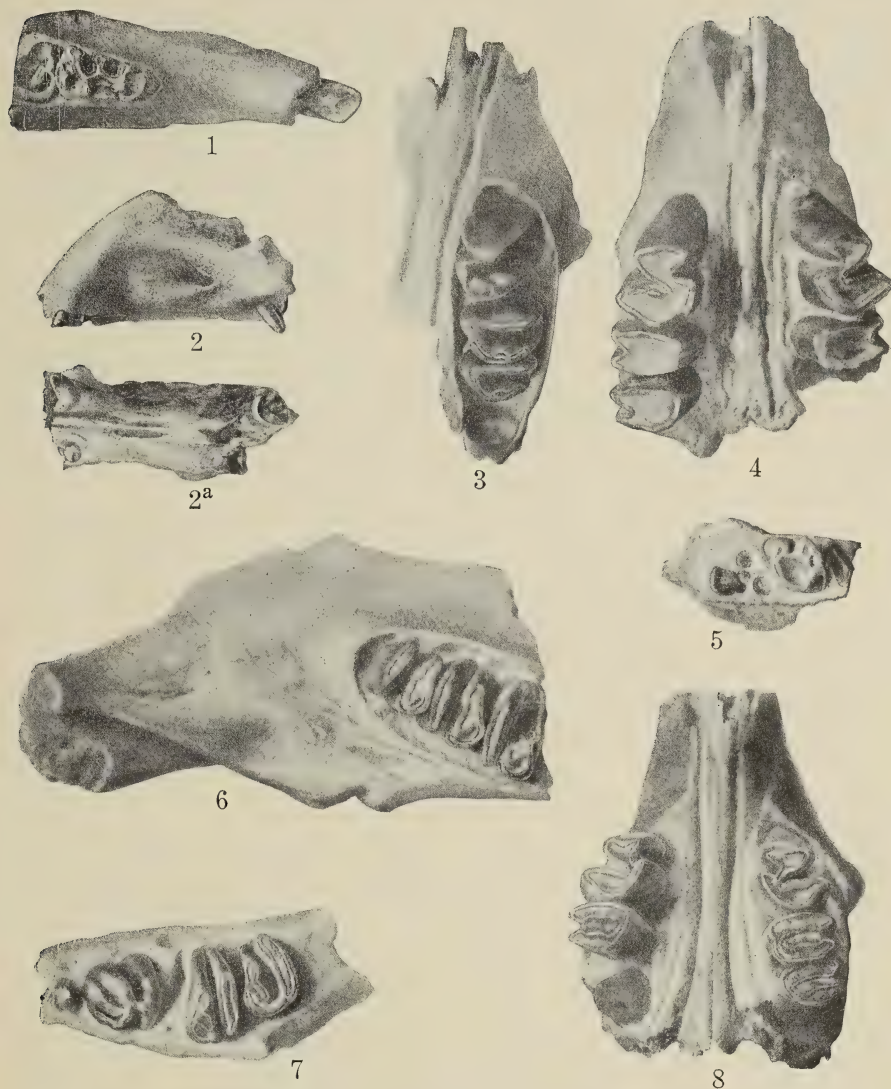
*Pliosaccomys dubius* n. gen. and n. sp.

FIG. 1—Fragmentary right ramus with DM $\bar{4}$ ; No. 1810; X6.

FIGS. 2, 2a—Rostral portion of skull, paratype specimen; No. 1797; X2. Fig. 2, lateral view; fig. 2a, ventral view (reversed).

FIG. 3—Right maxillary (reversed) with P $\bar{4}$ -M $\bar{2}$ ; No. 1800; X6.

FIG. 4—Maxillary with right P $\bar{4}$ -M $\bar{2}$ , left P $\bar{4}$ -M $\bar{1}$ , paratype specimen; No. 1798; X6.

FIG. 6—Fragmentary right ramus with M $\bar{1}$ -M $\bar{3}$ ; No. 1803; X6.

FIG. 7—Fragmentary left ramus with unworn P $\bar{4}$ , M $\bar{1}$ -M $\bar{2}$ ; No. 1809; X6.

FIG. 8—Maxillary with right P $\bar{4}$ -M $\bar{1}$ , left P $\bar{4}$ -M $\bar{2}$ ; No. 1799; X6.

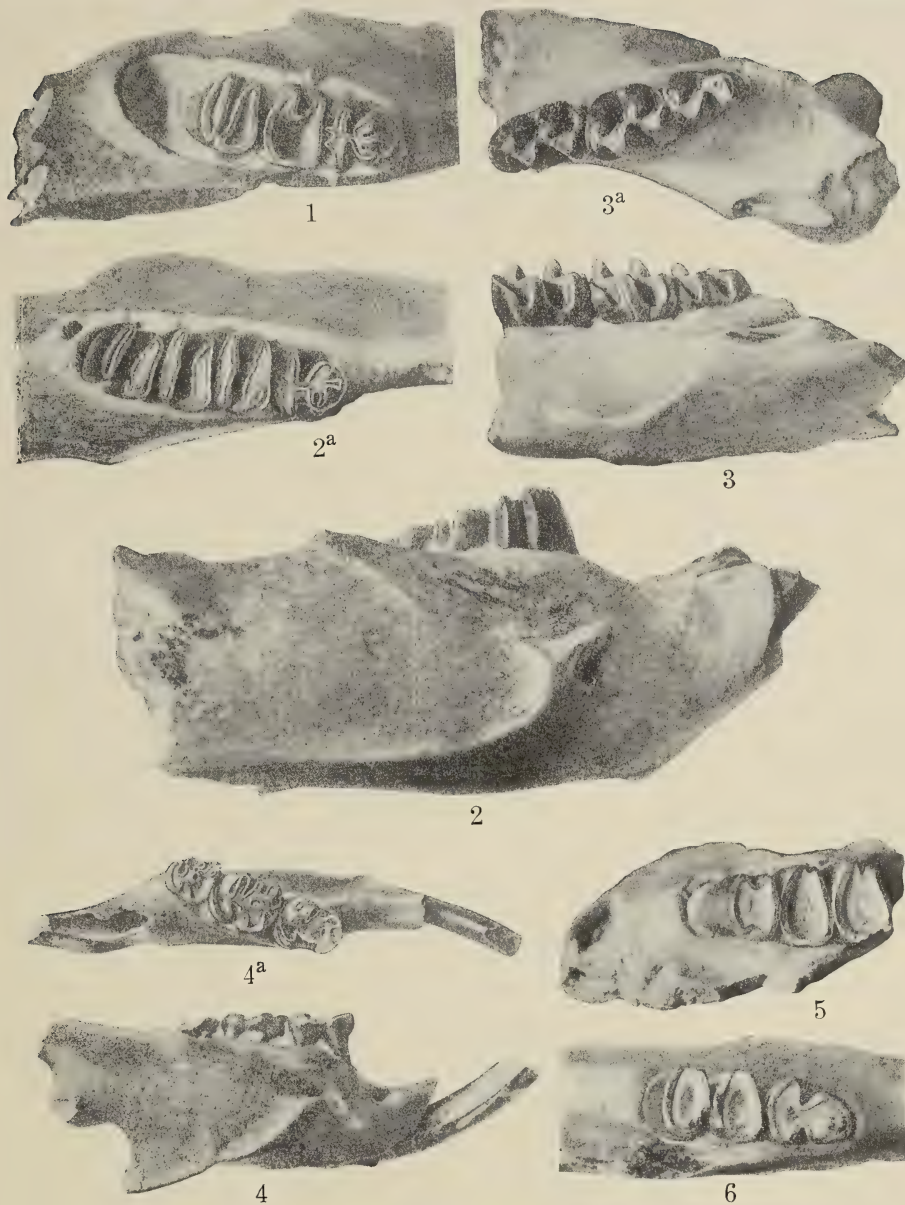
*Citellus?* species

FIG. 5—Fragmentary left ramus with M $\bar{2}$ ; No. 1794; X3.

Sizes of all figures approximate.

Calif. Inst. Tech. Coll. Vert. Pale. Pliocene, Smiths Valley, Lyon County, Nevada.





*Pliosaccomys dubius* n. gen. and n. sp.

FIG. 1—Right ramus with  $P\bar{4}$ – $M\bar{2}$ ; No. 1802; X6.

FIGS. 2, 2a—Right ramus with  $P\bar{4}$ – $M\bar{3}$ , genotype specimen; No. 1796; X6. FIG. 2, lateral view; fig. 2a, occlusal view.

FIG. 5—Fragmentary right ramus with  $M\bar{1}$ – $M\bar{3}$ ; No. 1806; X6.

FIG. 6—Right ramus with  $P\bar{4}$ – $M\bar{2}$ ; No. 1804; X6.

*Peromyscus* near *antiquus* Kellogg

FIGS. 3, 3a—Left ramus with  $M\bar{1}$ – $M\bar{3}$ ; No. 1812; X6. 3, lateral view; 3a, occlusal view.

*Pliozapus solus* n. gen. and n. sp.

FIGS. 4, 4a—Right ramus with  $M\bar{1}$ – $M\bar{3}$ , genotype specimen; No. 1811; X6. FIG. 4, lateral view; fig. 4a, occlusal view.

Sizes of all figures approximate.

Calif. Inst. Tech. Coll. Vert. Pale. Pliocene, Smiths Valley, Lyon County, Nevada.





CONTRIBUTIONS TO PALÆONTOLOGY

III

A PLIOMASTODON SKULL FROM THE THOUSAND  
CREEK BEDS, NORTHWESTERN NEVADA

By CHESTER STOCK

With one plate

Issued July 10, 1936





# A PLIOMASTODON SKULL FROM THE THOUSAND CREEK BEDS, NORTHWESTERN NEVADA

## INTRODUCTION

Mastodon remains are not uncommon in the Thousand Creek Pliocene beds of northwestern Nevada but the materials found thus far represent fragmentary and isolated specimens. Merriam<sup>1</sup> recorded the available specimens in 1911, including an incomplete skull which, unfortunately, was also poorly preserved. Because of lack of better material, determination of the mastodons has been unsatisfactory. Further collecting in these deposits in recent years by a field party of the California Institute of Technology yielded an incomplete skull. This specimen, found by Charles L. Gazin, furnishes an adequate basis for determining the relationships of the mastodon type occurring in the Thousand Creek fauna.

### *Pliomastodon nevadanus* n. sp.

*Type specimen*—No. 1922 Calif. Inst. Tech. Coll. Vert. Pale., an incomplete skull representing most of the palate. The dentition includes the second and third superior molars of each side and a complete right tusk.

*Specific characters*—*Pliomastodon nevadanus* is a small species, distinctly smaller than the Pleistocene American mastodon, *Mammot americanum*. It is likewise considerably smaller than *Pliomastodon vexillarius*. Tusk devoid of enamel and lacks the curvature seen in *M. americanum*. Cheek-teeth without cement. M<sub>2</sub> with three transverse crests; M<sub>3</sub> with four transverse crests and a rudimentary fifth crest.

*Locality*—Thousand Creek beds, Thousand Creek basin, approximately 4 miles northwest of the Hot Spring and on east side of Railroad Ridge, Humboldt County, Nevada.

## DESCRIPTION OF MATERIAL

The skull, No. 1922, evidently of a young adult, is shown in Plate 1, figures 1, 1a. The emergence of M<sub>3</sub> is not complete, but the characters of the crests in the posterior part of this tooth can be readily discerned. The anterior rim of the posterior nares lies opposite the fourth crest in M<sub>3</sub>. The palate between the third molars is narrow. Along the median line in this region extends a crest, which is thickened near the narial border and thins in its anterior extent. The posterior palatine foramen is situated on a level with the posterior crest of M<sub>2</sub>. In front of the second molar, the boundary between the palatal and lateral face of the skull is well defined and swings inward in its forward course, outlining a narrow space between it and the median line. The outward swing of this border near its forward end is not so pronounced as in the Pleistocene *Mammot*, and the distance

<sup>1</sup> J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 6, pp. 271-272, pl. 33, 1911.

between the forward end of M2 and the forward end of the skull is noticeably greater in the Thousand Creek specimen than in the latter genus.

In side view (fig. 1a) the tusk shows a nearly straight course, in which respect the Thousand Creek species differs from the North American Pleistocene mastodon. In the latter the tusk has a distinct curvature. No. 1922 differs likewise from *Pliomastodon vexillarius*, in which type the tusks give evidence of upward curvature and these teeth exhibit wider divergence near their base.

Viewed from below (fig. 1) the tusk shows only slight curvature in its forward course. The upper surface of the tusk is worn, particularly toward the forward end where cross-sections indicate clearly that the present upper surface truncates the concentric layers of dentine. The tusk in the Thousand Creek specimen is not so large in cross-section as that in *Miomastodon merriami* from the middle Miocene Virgin Valley beds. No enamel has been recognized on the former, but the section of tusk of *M. merriami*, as illustrated by Osborn,<sup>1</sup> possesses a broad band of enamel.

The maxillary portion of the skull immediately in front of M2 is either not present or poorly preserved, but the position of the border separating palate from lateral wall of skull makes it reasonably certain that M1 was absent. Loss of this tooth must therefore have occurred relatively early since M2 exhibits only moderate wear of crown. M2 is longer and narrower than the comparable tooth in *Mammut*. The crests are of moderate height and each consists of a transversely elongate cusp. A simple fold of the enamel extends forward from the outer anterior side of the inner cusp. The cingulum is best developed along the outer side of the first crest and on the posterior border of the crown. A small tubercle is present on the posterior cingulum behind the middle of the outer cusp. In M3 the crown possesses four cross ridges and a small heel consisting of two subequal cusps. The ridges are not so sharply crested as in *Mammut* and the small tubercles lying between the two principal cusps of each unworn ridge are a little more in evidence than in the Pleistocene genus. Viewed from the outer side (Plate 1, fig. 2) the individual ridge or crest is seen to be relatively narrow in fore and aft direction. No cement is present on the tooth crowns.

In the collections of the California Institute is a cast of a right upper molar 3, No. 92 Colorado Museum of Natural History, of *Miomastodon merriami* Osborn. Evidently the specimen, from which the cast was made, belongs to the type of the species recorded from the Virgin Valley beds of northwestern Nevada. However, no mention of this particular tooth is made nor is it illustrated by Osborn in his description of *M. merriami*. This tooth is smaller than M3 of *P. nevadanus*, the fourth crest is incomplete and is followed behind by a cingulum, and the transverse crests are lower. M3 in No. 1922 differs likewise in the more advanced character of the heel from a comparable tooth which forms the type of *P. matthewi*, No. 18237 Amer. Mus., from the Upper Snake Creek beds, Nebraska.

*Pliomastodon vexillarius* from the Etchegoin of the Kettleman Hills, California, comes from an horizon which is apparently nearly related in age to the Thousand Creek. Unfortunately, the cheek-teeth in this specimen are broken away. It represents a larger individual than No. 1922 and differs also in more marked divergence and in curvature of the tusks.

<sup>1</sup> H. F. Osborn, Amer. Mus. Nov. No. 10, fig. 2 E, 1921.

*Pliomastodon sellardsi* resembles *P. nevadanus* in size and may be closely related specifically to the latter. It is described by Simpson<sup>1</sup> from the lower Pliocene Bone Valley formation, Florida, and is known only by a lower jaw.

*Measurements (in millimeters)*

Length of tusk from tip to anterior end of skull.....	650
Length from anterior end of skull to posterior end of M3.....	500
Transverse diameter of tusk at third cross-section shown in Plate 1, fig. 1.....	61.4
Dorso-ventral diameter of tusk at third cross-section shown in Plate 1, fig. 1.....	46.8
M2, anteroposterior diameter .....	112
M2, transverse diameter across third crest.....	71.7
M2, height of third crest above valley.....	30
M3, anteroposterior diameter .....	155.6
M3, greatest transverse diameter .....	76
M3, height of second crest above valley.....	32.5

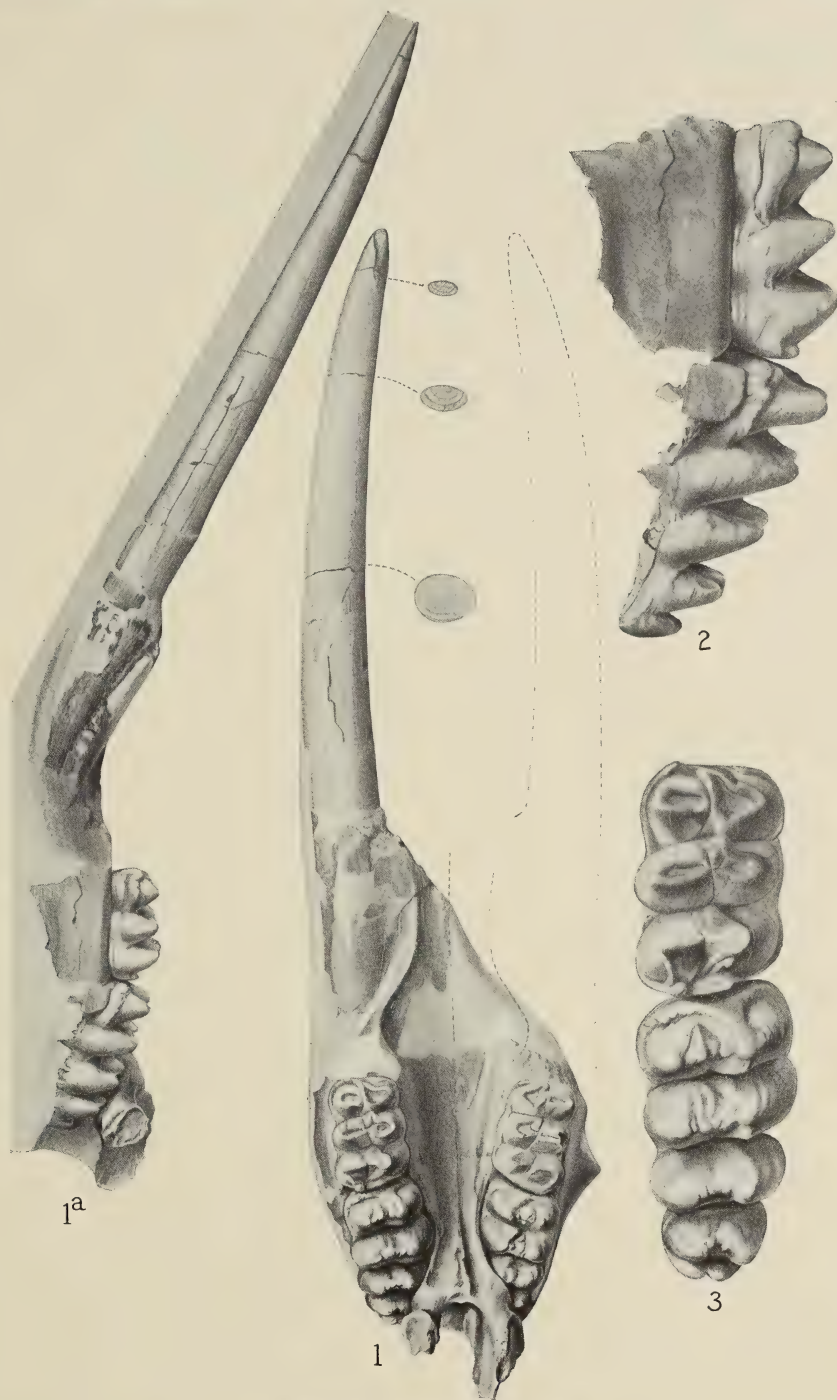
### CONCLUSIONS

Although the genus *Pliomastodon* was proposed by Osborn in 1926 and its principal character defined as being an absence of lateral enamel bands on the incisor tusks, no specimen referred to this genus has been sufficiently well preserved to demonstrate the validity of this character. An incomplete skull from the Pliocene Thousand Creek beds, northwestern Nevada, possesses the superior cheek-teeth and one tusk. The latter shows no evidence of an enamel band. The specimen is described as belonging to a new species, for which the name *Pliomastodon nevadanus* is proposed. It is clearly distinct from, and more advanced than, the mastodon (*Miomastodon merriami*) from the Virgin Valley deposits.

<sup>1</sup>G. G. Simpson, Bull. Amer. Mus. Nat. Hist., vol. 59, art. 3, pp. 203-206, figures 30, 31, 1930.







*Pliomastodon nevadanus* n. sp.

Figures 1, 1a, No. 1922, incomplete skull with upper dentition (left tusk missing), inferior and lateral views;  $\times 2/15$ .

Figures 2, 3, No. 1922, right M<sub>2</sub> and M<sub>3</sub>, lateral and occlusal views;  $\times 4/15$ .

California Institute of Technology Collections. Thousand Creek Pliocene, Northwestern Nevada.





CONTRIBUTIONS TO PALÆONTOLOGY

IV

MUSTELID MAMMALS FROM THE PLEISTOCENE  
OF NORTH AMERICA

With

SYSTEMATIC NOTES ON SOME RECENT MEMBERS OF THE  
GENERA MUSTELA, TAXIDEA AND MEPHITIS

By E. RAYMOND HALL

With five plates and six text-figures

[Issued November 20, 1936]

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† Extinct forms.

Species and subspecies listed above and not marked with a † are known from remains of both Pleistocene and Recent age.

# MUSTELID MAMMALS FROM THE PLEISTOCENE OF NORTH AMERICA

## INTRODUCTION

In the course of a study of Recent and fossil Mustelidæ, opportunity has been taken to examine the greater part of the Pleistocene material described from North America. The results of this examination are offered here in advance of an account of all the North American fossil forms, as meeting the requests of other students now actively at work on problems relating to mammalian faunas of the Pleistocene.

Though sharing with these several other workers, as any mammal student must, a genuine interest in the problems of the Pleistocene, I confess that I have approached the present task more from the point of view of the student of Recent mammals than from that of the palæontologist. This point of view involves among other things a large measure of skepticism as to the validity of any "new species" based on one or a few specimens and distinguished by slight morphological features not reproduced in a random sample of the living species. Experience with Recent mammals in series quickly teaches one that individual variation may be of large amount, that secondary sexual variation, sometimes amounting to as much as fifty per cent in mass of skull in one kind of mammal, may be practically non-existent in another closely related genus or species, and that geographic variation imposed on all this has limits so wide that two populations of a single species may constantly differ from one another, qualitatively as well as quantitatively, in a degree that would induce the systematist to refer the two to distinct species, even to separate subgenera, if the intermediate populations from intervening areas were not known. Obviously, therefore, even with the fact established that animals of a certain kind, A, from a Pleistocene deposit differ morphologically from a closely related species, B, living in the same region today, we have to consider among other possibilities that A, instead of being an extinct kind, may be a subspecies of B found today in a region more or less remote from the deposit of fossils.

Then, too, in studying the remains of these creatures, I admittedly have been more directly interested in the phylogeny of the animal groups than in the strata in which they are found. Remembering this major interest, and the writer's approach to the present study, the reader may more accurately gauge the conclusions arrived at with respect to certain species and understand the principal aims, which are:

(1) To ascertain the kinds of mustelids found in North American Pleistocene deposits;



- (2) To arrange these kinds under the earliest available names; and
- (3) To provide a complete index to the published literature treating of each particular kind.

In attempting to realize the first two aims, constant reference was made to Recent materials. Since our knowledge of the Recent kinds of several genera of the Mustelidæ is notably imperfect, it has been necessary to include some material, in itself of interest primarily to the systematic student, of living kinds of mammals. However, this has been reduced to the essentials—diagnoses of a few new geographic races and revised classifications within some genera—required for accurate nomenclatural handling of the fossil material. This should be understood as preliminary to more detailed statements of results of studies under way on these groups, particularly with respect to remarks on the subgenus *Mustela*.

#### ACKNOWLEDGMENTS

The present study had its inception more than ten years ago when as a student of Professor Chester Stock my interest was stimulated by him in the Pleistocene mustelid remains from cave deposits of California. Many other individuals and several institutions have furnished materials or rendered assistance in the progress of this work. Of these I would select for special mention Miss Annie M. Alexander, Professor Joseph Grinnell, and the National Research Council. Miss Alexander's provision through the years of highly favorable working conditions, Professor Grinnell's assistance in the many ways that a sympathetic senior can encourage a younger worker, and a substantial grant from the National Research Council, have combined to bring the writer's study of the Mustelidæ much nearer completion than it otherwise would be. Most of the illustrations were prepared by Mrs. Frieda L. Abernathy, though text-figure 6 was drawn by Miss Margaret Wythe, and figures 1, 2, 4, and 5 of Plate 2, and figure 2 of Plate 3, and text-figures 1, 2, and 4 were done by Mr. John L. Ridgway.

#### GENERAL CONSIDERATIONS

In all, 9 genera of Mustelidæ are known from North American deposits regarded by one or several writers as of Pleistocene age. Two of these genera, *Brachyprotoma* and *Osmotherium* are extinct. Two Recent genera, *Enhydra* and *Conepatus* have not been recorded from North American Pleistocene deposits. Of the seven living genera known from the Pleistocene, *Spilogale*, *Martes* and *Mustela* are represented by both extinct and living species. *Gulo* is represented only by an extinct species. *Mephitis*, *Lutra* and *Taxidea* are represented only by living species.

Of the fifteen species<sup>1</sup> known from the Pleistocene, 6 are extinct, 9 are living. Two of the living species (of *Mustela*) have both extinct and living subspecies. One of the extinct species, *Mustela macrodon*, has not been found in beds surely known to date back to Pleistocene time.

Three of the nine living species have been found in Pleistocene deposits far outside their ranges as known within historic time. *Taxidea taxus*, found in the Pleistocene of Pennsylvania and Maryland, now occurs eastward only as far as Ohio. *Martes pennanti*, known from the Pleistocene of northern Arkansas, now reaches southward only to Michigan. *Mustela cicognanii*, also from the Pleistocene of northern Arkansas, now occurs only much farther to the north. The remaining six living species are found at, or are known to have occurred within historic time very near to, localities where their fossil remains were recovered.

None of the extinct Pleistocene forms can be definitely regarded as ancestral to a Recent one. The extinct genera *Brachyprotoma* and *Osmotherium* almost certainly were not ancestors of any living mustelids. With almost equal certainty the same can be said of *Mustela macrodon*. The remaining five extinct forms, two subspecies of as many living species of the subgenus *Mustela*, and the extinct species *Spilogale marylandensis*, *Gulo gidleyi*, and *Martes diluviana*, might, insofar as morphological features are concerned, be ancestral to living forms, but I find no proof or even strong indication that this is the case.

Although no measurable change has been recognized in any direct descent line among North American Quaternary Mustelidæ, suggestions of such change are not lacking. In the Pleistocene of the eastern United States are found the extinct species *Spilogale marylandensis*, *Gulo gidleyi* and *Martes diluviana*, each occurring alone, that is to say, not together with their Recent counterparts, *Spilogale putorius*, *Gulo luscus* and *Martes pennanti*. Also, each of these fossil species is smaller (except possibly the *Spilogale*) than the comparable living species. In comparing remains of these and of other forms, notably *Mustela vison* from Pleistocene deposits, the problem is to find Recent specimens as small as the fossils. In only one instance (*Lutra*) was the problem one of finding Recent specimens as large as those from the Port Kennedy and Cumberland Cave deposits. This suggests that an increase in size has occurred among these animals during the Quaternary. However, materials from deposits in the western United States (caves in Shasta County and asphalt deposits at Rancho La Brea, California) suggest that the Pleistocene ani-

<sup>1</sup> Counted as one species are Recent forms of *Spilogale*; two *Martens* (*M. americana*, *M. caurina*).



mals were larger than the Recent ones. At any rate, whenever the character of size presented itself in a comparison of fossil and Recent remains from these western localities, the problem always was to find Recent specimens as large as the fossils. *Martes caurina* from Potter Creek Cave and *Mustela frenata* from Rancho La Brea are cases in point. The suggestion, then, is that during the Pleistocene, mustelids in the east were smaller than their living representatives and in the west larger than their living representatives.

	Port Kennedy Cave, Penn.	Cumberland Cave, Md.	Conard Fissure, Ark.	Rancho La Brea, Calif.	Potter Creek Cave, Calif.
† <i>Brachyprotoma obtusata</i> .....	E	E	E		
† <i>Spilogale marylandensis</i> .....		E			
Spilogale (Recent form).....			R	R	R
† <i>Osmotherium spelæum</i> .....	E				
<i>Mephitis</i> (Recent form).....	?		R	R	R
<i>Lutra</i> (Recent form).....	R	R			
<i>Taxidea</i> (Recent form).....	R*	R*		R	R
† <i>Gulo gidleyi</i> .....	E	E			
<i>Martes</i> (Recent marten).....					R
<i>Martes pennanti</i> (Recent form).....			R*		
† <i>Martes diluviana</i> .....	E	E			
† <i>Mustela cicognanii angustidens</i> .....			E		
† <i>Mustela frenata gracilis</i> .....			E		
<i>Mustela frenata</i> (Recent forms).....				R	R
<i>Mustela vison</i> (Recent forms).....		R	R		
Extinct forms.....	4	4	3	0	0
Recent forms.....	2	3	4	4	5

† and E refer to extinct forms.

R refers to Recent forms.

\* denotes Recent forms not found in same region today.

If such differences actually exist, a possible explanation is that the deposits of the two regions, east and west, are of distinctly different age. One recalls that no extinct genera, or even extinct species, of Mustelidæ are known from the western deposits. Possibly the western Pleistocene assemblages were entombed, as some have claimed, at a later time than those in the eastern United States. The differing compositions of mustelid faunas alone as found in the five well-known Pleistocene assemblages compared above might well be explained by assuming greatest age for those of the eastern United States, least age for those in California, and an intermediate age for that in Arkansas. These suggestions of course are highly tentative. Consideration of each assemblage as a whole gives basis for more reliable estimates of age of the deposits.



## SPECIES AND SUBSPECIES NEWLY NAMED IN THE PRESENT PAPER

† <i>Gulo gidleyi</i>	†* <i>Mustela frenata latirostra</i>
†* <i>Mustela frenata nevadensis</i>	* <i>Mustela frenata pulchra</i>
* <i>Mustela frenata effera</i>	* <i>Mustela frenata inyoensis</i>
* <i>Mustela frenata altifrontalis</i>	* <i>Mustela frenata texensis</i>
†* <i>Mustela frenata nigriauris</i>	* <i>Mustela frenata perotæ</i>

† Fossil.

\* Recent.

## DESCRIPTION OF MATERIALS

## Genus BRACHYPROTOMA Brown

Hay (1905, p. 300, *nomen nudum*); Brown (1908, p. 176); Osborn (1909, p. 90; 1910, pp. 488, 531); Matthew (1915, p. 402); Zittel (1925, p. 73); Pilgrim (1933, pp. 2-14).

*Diagnosis*—Skull short, basilar length near 40 mm.; facial angle steep, near that of *Conepatus*; mastoid bullæ not inflated; posterior margin of palate nearly on a line with posterior margins of last molars; transverse and especially anteroposterior diameter of M<sub>1</sub> less than outside length of P<sub>4</sub>; dental formula  $\frac{3}{3} \frac{1}{1} \frac{2}{2} \frac{1}{1}$ ; infraorbital canal opening above anterior half of

P<sub>4</sub>; metaconule of M<sub>1</sub> absent; inferior margin of mandible relatively straight; angle of mandible not expanded in flat plane vertically or horizontally but globular and not producing "step" or concavity seen in *Mephitis*; coronoid process high and vertical or inclined posteriorly; in M<sub>1</sub> trigonoid longer than talonid, metaconid low and appressed to protoconid, hypoconid high, entoconid high (but lower than in *Mephitis*), long, and separated from protoconid by a deep notch. (See Plates 1, 2 and 3.)

*Genotype*—*Brachyprotoma pristina* Brown, 1908.

*Remarks*—*Brachyprotoma* is known from four deposits, each of Pleistocene age, as follows: Cumberland Cave, four miles northwest of Cumberland, Maryland; Port Kennedy bone deposit, Montgomery County, Pennsylvania; Frankstown Cave, Blair County, Pennsylvania; and Conard Fissure, Newton County, Arkansas. All materials reported upon from these places have been examined by the present writer, except those from Port Kennedy which are now lost. Indeed no specimen answering Cope's description of *Mephitis obtusatus* was found by those who saw his posthumous paper through the press. (See Cope, 1899, p. 236, footnote.)

In addition to the characters mentioned above, the genus *Brachyprotoma* is characterized, as clearly set forth by Brown (1908, pp. 176-179), by the short broad face with reduced postorbital processes, small size of the anterior opening of the infraorbital canal, crowded, overlapping lower premolars, and abrupt, deep mandibular symphysis. Quoting from Brown (1908, p. 178):

"Posterior nares not nearly as wide as the distance between the anterior margin and the molar teeth. The foramen which opens from immediately behind the cribriform plate into the orbital cavity is much larger than in living genera. Optic foramen similar to *Spilogale*. Sphenoidal fissure relatively large and rounded without indication of septum separating it from foramen rotundum. Foramen ovale . . . is proportionately smaller than in living genera. Foramen lacerum jugulare, or posterius, large, while the condyloid foramen close to it is smaller than in *Spilogale*. Carotid foramen

large and far forward, close to eustachian canal as in *Conepatus*. . . . The last [lower] molar is minute, much smaller proportionally than in *Spilogale*, simple, circular, single rooted, with a central depression and irregularly raised margin. . . . Owing to the crowding of the premolars, the dental series are curved more than in living skunks."

Excluding *Promephitis* of the Old World, greater difference prevails between *Brachyprotoma* and any other genus of the Mephitinæ than exists between any other two genera of this subfamily.

Probably *Brachyprotoma* did not linger on in the Pleistocene much later than, if as long as, the time of retreat of the last ice sheet. In each of the four localities where found, *Brachyprotoma* is associated with animals now of northern or boreal distribution. Whether or not it was contemporaneous with *Mephitis* is not entirely clear, but apparently the two did occur together. Peterson (1926) found one specimen of *Mephitis* in the Frankstown Cave. Brown found *Mephitis* in the Conard Fissure, but this, it appears to me, may have represented a later intrusion. *Mephitis* has not been reported from Cumberland Cave. All material seen from the Port Kennedy bone deposit is of the genus *Osmotherium* and not *Mephitis*, although Cope (1899, p. 232) hinted at the existence of *Mephitis* remains with those of *Brachyprotoma obtusatus* when he said:

"There are jaws and teeth of at least fifty-five individuals of the genus *Mephitis* in the collection obtained by Mr. Mercer. Of these I can determine, as to specific character, twenty-four. All belong to extinct species except perhaps two fragments of upper jaws, which contain the tubercular molars and other teeth, the former resembling the corresponding tooth of the existing skunk; no lower jaws of this species have, however, been found, so that the reference cannot be certainly made."

The allusion by Cope (1899, p. 237) to similarity in size between *M. obtusatus* (= *Brachyprotoma*) and *Putorius* (= *Mustela*), and Brown's (1908, p. 176) statement that—"The transverse elongation of the upper molar and reduction of the metaconid in the lower carnassial are characters that show this genus to have been more closely related to the weasels than are any of the living skunks."—is not to be interpreted as evidence of any close relationship between the weasels and skunks, for *Brachyprotoma* definitely was a skunk-like and not a weasel-like animal. This relationship, of course, was recognized by both Cope and Brown.

The slightly more trenchant M<sub>1</sub> and anteroposteriorly narrower M<sub>1</sub> of *Brachyprotoma* in comparison with that of *Mephitis* or *Spilogale* may represent merely the retention of a primitive form rather than a specialization toward an improved type of flesh-eating dentition. In that case the transversely wide and closely set pavement of premolars might point toward a diet which included many hard-shelled insects. It is difficult to envisage so small a carnivore employing these hyæna-like premolars in the same way that the teeth are utilized by the hyæna, namely for bone-crushing. In the premolars of *Brachyprotoma*, be it remembered, not only are the roots transversely situated, which condition may follow from a shortening of the anterior half of the jaw, but in addition the talonid portions of the premolars are expanded in a fashion difficult to associate, in direct causal relationship, with shortening of the anterior part of the jaw.



*Brachyprotoma obtusata* (Cope)

## Plates 1, 2, 3

- Mephitis obtusatus* Cope (1899, p. 236); Howell (1901, p. 19); Rhoads (1903, p. 230); Baker (1920, pp. 208, 215, 397).  
*Mephitis obtusata*, Hay (1902, p. 766); Trouessart (1904, p. 192); Hay (1923, p. 312).  
*M. [ephitis] obtusatus*, Schlosser (1902, p. 142) review of Cope (1899).  
*Brachyprotoma obtusatus*, Brown (1908, p. 177).  
*Brachyprotoma obtusata*, Peterson (1926, p. 285, fig. 7); Hay (1930, p. 532).  
*Brachyprotoma pristina* Brown (1908, p. 177, pl. 16); Hay (1914, p. 32; 1924, p. 252); Peterson (1926, p. 285); Hay (1930, p. 532); Pilgrim (1933B, pp. 11, 12); Gidley and Gazin (1933, p. 344).  
*Brachyprotoma putorius*, Hay (1923, p. 322), *lapsus calami* (?) for *Brachyprotoma obtusata*.  
*Brachyprotoma spelæa* Brown (1908, p. 179, pl. 16); Hay (1914, p. 32); Hay (1924, p. 252; 1930, p. 532).

*Type*—"Nearly entire right mandibular ramus, which has the condyle, angle, and symphysis complete, and all the molars excepting the  $pm\bar{2}$  [=  $P\bar{3}$ ] and  $m\bar{2}$ . Canine alveolus complete." After Cope (1899, p. 236). From the Port Kennedy bone deposit (Pleistocene age), right bank of Schuylkill River, two miles below Valley Forge, Upper Merion Township, Montgomery County, Pennsylvania. The type specimen has not been examined by the writer and its present location is unknown.

*Referred specimens*—No. 11057 consisting of a left lower jaw lacking the canine and that part of the jaw anterior to it, a right lower jaw lacking the incisors and all that part of the jaw posterior to  $M\bar{1}$  and a left upper incisor; No. 11058, section of left lower jaw bearing  $P\bar{3}$  to  $M\bar{1}$  inclusive; an unnumbered, edentulous section of a right lower jaw, comprising that part from the anterior root of  $M\bar{1}$  to and including the symphysis but lacking the alveoli of the incisors; a right lower canine, without catalogue number; No. 11057a, fragment of right maxilla bearing  $M\bar{1}$ ,  $P\bar{4}$  and the anterior opening of the infraorbital canal; all in the Carnegie Museum, and collected by O. A. Peterson in 1907 in the Frankstown Cave deposits (Pleistocene age), on the Juniata, one-fourth mile from Frankstown, Blair County, Pennsylvania. From Cumberland Cave, four miles northwest of Cumberland, Maryland, and now in the United States National Museum, No. 8155, skull lacking left zygomatic arch, canines, left incisors, and right  $P\bar{3}$ ; No. 11960, anterior portion of skull bearing on each side  $P\bar{4}$  and roots of  $P\bar{3}$ , also right  $M\bar{1}$  and root of left  $C\bar{1}$ ; No. 8165, left lower jaw bearing  $P\bar{4}$ ,  $M\bar{1}$  and alveolus of  $M\bar{2}$ , but lacking angular, articular and most of coronoid processes; No. 12045, left lower jaw lacking incisors, tip of canine and tip of coronoid process; No. 12046, left lower jaw, bearing  $P\bar{2}$  to  $M\bar{1}$ , alveoli of  $M\bar{2}$  and canine, but lacking incisors, angular, articular and coronoid processes; No. 8214, right lower jaw bearing  $P\bar{4}$ ,  $M\bar{1}$ , alveoli of canine,  $M\bar{2}$ ,  $P\bar{2}$  and  $P\bar{3}$ , but lacking tip of coronoid process. From Conard Fissure, four miles west of Willockson, Newton County, Arkansas, collected some time between 1903 to 1905 inclusive, and in the American Museum of Natural History, the following: No. 12462, anterior half of skull bearing on each side  $P\bar{4}$  and  $M\bar{1}$ , and the alveoli of the other teeth save those of the incisors; three lower jaws, No. 11773, complete except for the incisors, canines and in one case  $M\bar{2}$ ; No. 11772, underside of one skull (see figure); and No. 12399, a right lower jaw of a young individual bearing  $P\bar{3}$ ,  $P\bar{4}$ ,  $M\bar{1}$  and the alveoli of the other teeth.

*Diagnosis*—A single species known to which, therefore, characters as given for the genus may be applied.



*Remarks*—The names *Brachyprotoma spelæa* and *Brachyprotoma pristina* were based on material from the same deposit (see Brown, 1908). Since *B. spelæa* is known only from a single lower jaw, No. 12399, A. M. N. H., comparison with *B. pristina* is limited to the three known lower jaws, Nos. 11733\*, a, and b, of the latter species.

That the jaw of *B. spelæa* is of a young individual is clearly shown by each of the following features: Unworn teeth, rounded porous condition of the angle and dorsal border of the coronoid process where the temporal and masseteric muscles attach most firmly, and the characteristic separation of the alveolar walls from the cheek-teeth. By reason of showing conditions of maturity in all of these parts, each of the three jaws of *B. pristina* is seen to pertain to an adult animal. This immaturity of *B. spelæa* having been established, the shallower, more delicate lower jaw in comparison with the three adult specimens of *B. pristina* would be expected by analogy with *Mephitis*. The same holds true for the shallower masseteric fossa and shorter antemolar section of the jaw. Corresponding differences, in greater degree, exist between two specimens of *Mephitis mephitis occidentalis* before me. These two specimens in the collection of the Museum of Vertebrate Zoology are No. 18478, a young male of about the same age as the type specimen of *B. spelæa*, and an adult, No. 21135. (See figure 1, a, b.) The difference in inclination of the ascending ramus as measured along its anterior border is slightly less than that between a young female of *M. m. occidentalis*, No. 38854, and an adult female, No. 24417, of the same subspecies. (See fig. 1, c, d.) This difference in inclination of the coronoid process appears, however, to be due in part to individual variation as well as to age variation.

MI of *B. spelæa* is only two-tenths of a millimeter shorter, and less than one-tenth of a millimeter narrower, than the corresponding tooth in No. 11773b of *B. pristina*. If the width be divided by the length, the teeth of the two specimens are seen to be of the same relative proportions. The slenderness of MI in *B. spelæa* is, then, apparent rather than real. Among the four specimens of *Brachyprotoma* under discussion, it develops that the index of the width of MI, obtained by dividing its length into the width at the metaconid, varies from 40 to 46, whereas in a series of 36 specimens of *Mephitis mephitis occidentalis*, this index varies from 38 to 44, or exactly to the same amount. If the width of MI be taken across the talonid, the index varies from 35 to 39 which is less than half as much as in *M. m. occidentalis*, where the variation is 37 to 46. The differences here discussed include all those assigned by Brown (1908) to *B. spelæa* as distinguishing it from *B. pristina*. Since no other differences not covered by variation due to age, sex or individualism in the thirty-seven specimens of the single Recent subspecies *Mephitis mephitis occidentalis* have been discovered, it seems necessary, at least with the present material, to regard the *Brachyprotoma* of Conard Fissure as belonging to a single species. The name *Brachyprotoma pristina* has two-page priority over *Brachyprotoma spelæa*, which becomes a synonym of the former.

As regards *Mephitis obtusatus* Cope in comparison with *Brachyprotoma pristina*, little can be said of the material, now lost, on which the name *obtusatus* originally was based, beyond the fact that it clearly was of the genus *Brachyprotoma* Brown. Cope's (1899, p. 236) mention of small size (measurements probably subject to 20 per cent correction) and shape of the angle of the lower jaw is diagnostic. However, two statements in his description (*loc. cit.*) almost surely are subject to correction. One is his

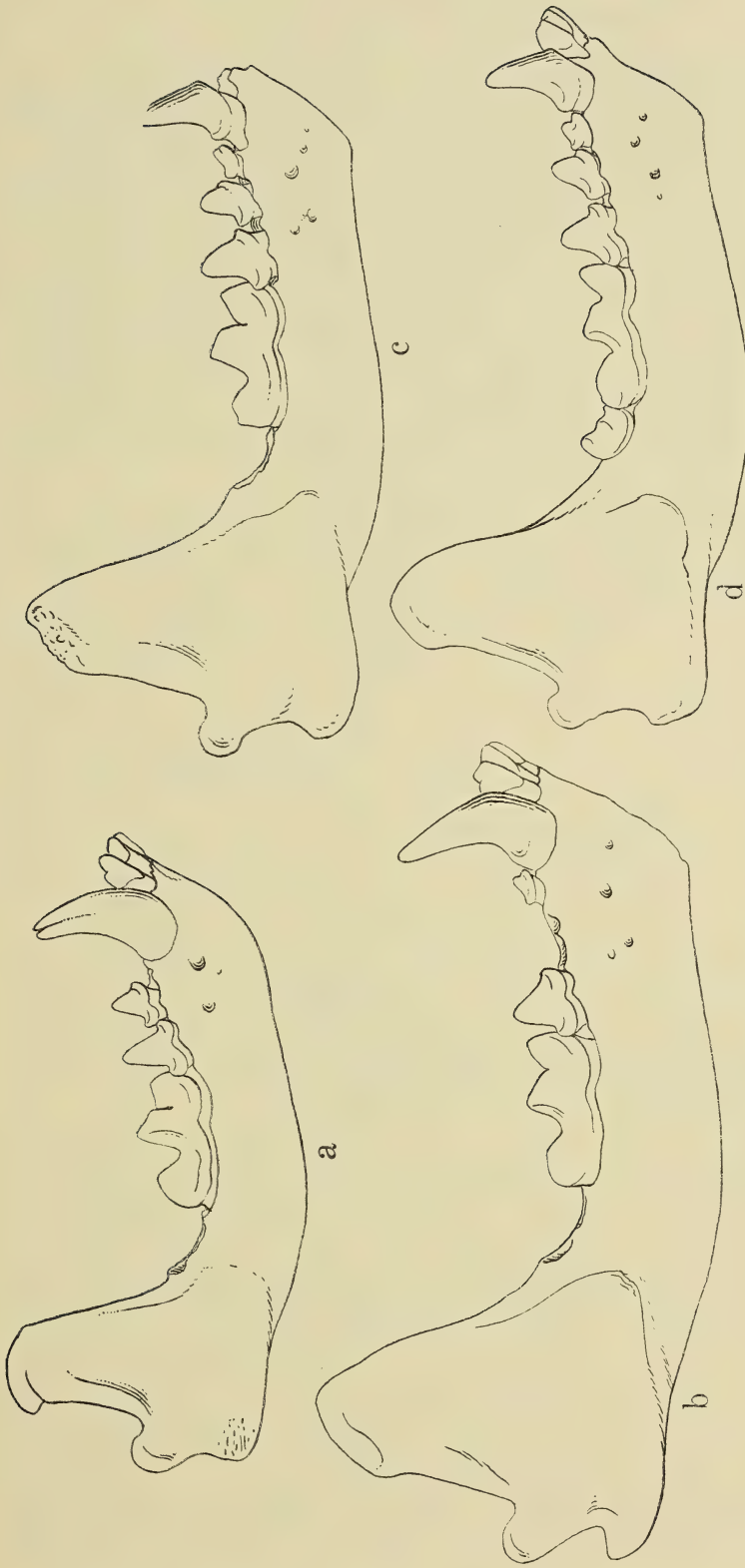


FIG. 1.—Four right lower jaws of *Mephitis mephitis occidentalis* Baird to show variation of form.  $\times\%$ . In a and b note difference in relative length of antemolar section of tooth-row and in relative depth of masseteric fossa. In c and d note difference in inclination of anterior margin of ascending ramus.

- a. Young male, No. 18478, Mus. Vert. Zool.; Vacaville, California.
- b. Adult male, No. 21135, Mus. Vert. Zool.; Carlotta, California.
- c. Young female, No. 38854, Mus. Vert. Zool.; 6 miles north of Courtland, California.
- d. Adult female, No. 24417, Mus. Vert. Zool.; Mount Tamalpais, California.



statement "... the form of the ramus, ... is like that of *M. leptops*." By this statement he intended to bring out the fact that the inferior margin of the ramus was relatively straight, but as set forth in the account of *Osmotherium spelæum*, Cope misjudged the shape of the inferior margin of the lower jaw in *Mephitis leptops* because of an unappreciated amount of breakage. At any rate, the two rami of *M. leptops* were those of two very young individuals. Also, Cope's statement that "The sectorial is a diminutive of that of *M. orthostichus*, having the same low metaconid and entoconid" almost certainly is misleading in that, although the metaconid and sometimes the entoconid are similar in the two forms, the construction otherwise is not similar but, instead, differs as set forth in the generic diagnoses of *Osmotherium* (includes *M. orthostichus*) and *Brachyprotoma* (includes *M. obtusatus*). The mentioned similarity in relative (to post premolar) length of the premolar-bearing section of the jaw in *M. obtusatus* and *M. leptops* reflects the immaturity of *M. leptops*. Otherwise Cope's account of *M. obtusatus* might well be correct.

However, there is further basis for judging of the characters of *M. obtusatus*. This comprises the material from Frankstown Cave, also in Pennsylvania, which answers to Cope's description of *M. obtusatus*. Careful comparison of these specimens with those from the Conard Fissure of Arkansas reveals no differences judged to be of unquestionable systematic worth. True, there are differences. One is the greater average length of M1 in the Pennsylvanian specimens. Another is the more nearly straight inferior margin of the lower jaw in the single Pennsylvanian specimen showing this part. A third is the greater enlargement of the posterodorsal part of the coronoid process in the single specimen showing this part. The two differences first mentioned are of lesser importance than those found in single subspecies of nearly related genera. The third may reflect, in part, the lesser age of the Frankstown specimen. It is younger than the three adults from Conard Fissure, as judged by the wear of the teeth. Also, similar differences exist as between young and old specimens of *Mephitis* of the same race. Even so, the wide geographic separation of the Arkansan and Pennsylvanian materials would lead one to suspect that subspecific distinctions might exist between animals from the two areas even if the faunas were exactly contemporaneous. Also the three mentioned differences may be of systematic worth as well as characters of age. However, until more material of the same ontogenetic stage is available from the two areas, employment of more than one name seems unjustified.

Since writing the above I have been privileged to examine, through the courtesy of Dr. C. L. Gazin, the four lower jaws of *Brachyprotoma* from Cumberland Cave and am more strongly than before of the opinion that only one name should be applied to all the material here referred to the genus *Brachyprotoma*. The specimens from Cumberland Cave bridge the gap between those from Arkansas and Pennsylvania in their morphological characters. As may be seen from the measurements, given below, M1 in some of the Cumberland Cave specimens is as short as that in the Arkansan specimens, while the tooth in other specimens is as long as that in the fossil jaws from Pennsylvania. The inferior outline of the mandible is less nearly straight than in the specimen from Frankstown Cave but less irregular than in those from Conard Fissure. Similarly, as shown in plates 1, 2 and 3, the ascending ramus of the mandible is intermediate in degree of inclination in specimens from the Cumberland Cave deposit.

Hay (1923, p. 322) states that his name *Brachyprotoma putorius* for an animal from the Frankstown Cave was furnished by Peterson in a manu-



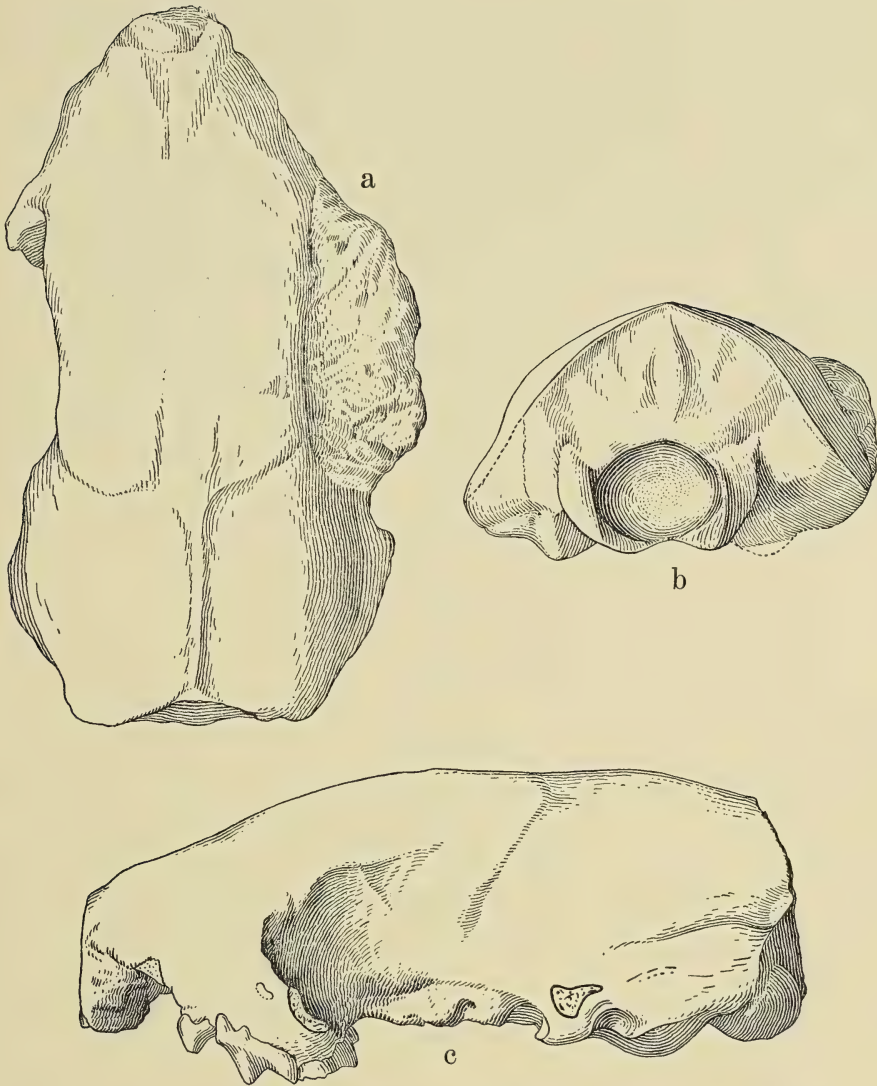


FIG. 2—*Brachyprotoma obtusata* Cope, skull, No. 8155, U. S. Nat. Mus.; Pleistocene, Cumberland Cave, Maryland.  $\times 2$ . a, dorsal view; b, occipital view; c, lateral view.

script list. However, Peterson three years later (1926, p. 285, fig. 7) correctly designates the material from this locality as *Brachyprotoma obtusata* and makes no mention of the species *putorius*. Probably the two names refer to the same material.

#### Genus SPILOGALE Gray

Gray, Proc. Zool. Soc. London, 1865, p. 150.

*Diagnosis*—Skull small, ranging in basilar length from 35 to 56 mm.; flattened in longitudinal dorsal outline, of nearly equal height in parietal and frontal regions; mastoid bullæ highly inflated; palate nearly on a line

Measurements in millimeters of twelve lower jaws of *Brachyprotoma obtusata* (Cope)

The first four are from Conard Fissure, Arkansas, and are in the collection of the American Museum of Natural History. The second four are from Frankstown Cave, Pennsylvania, and are in the collection of the Carnegie Museum. The last four are from the Cumberland Cave Deposit, Maryland, and are in the United States National Museum.

Catalog No.	Ontogenetic age	Length of jaw from lateral tip of condyle to anterior end	Depth of jaw at posterior corner of canine	Alveolus of canine width x length	Depth of jaw at anterior border of M <sub>1</sub>	Depth of jaw at posterior border of M <sub>1</sub>	Length of M <sub>1</sub>	Length of trigonid, measured from posterior border of protoconid, and not from notch between talonid and trigonid	Width of M <sub>1</sub> through base of metaconid	Width of M <sub>1</sub> across talonid	Outside length of P <sub>4</sub>	Width of heel of P <sub>4</sub>	Alveolar lengths except at the posterior border of P <sub>4</sub>		
													Posterior border of P <sub>4</sub> to anterior border of P <sub>3</sub>	Posterior border of P <sub>4</sub> to anterior border of canine	Posterior border of P <sub>4</sub> to anterior border of P <sub>3</sub>
12399	young	26.7	6.2	2.6 x 2.6	4.9	4.6	6.9	4.3	2.80	2.4	3.0	2.5	5.4	7.9	4.5
11773*	adult	29.9	7.1	3.0 x 3.0	5.9	5.4	7.0	4.45	3.20	2.7	3.3	2.7	5.4	8.3	4.9
11773a	adult	30.7	7.2	2.8 x 2.8	5.7	5.4	7.1	4.5	3.05	2.7	3.2	2.9	5.9	9.2	5.2
11773b	adult	29.8±	6.9	.....	5.8	5.4	7.1	4.5	2.85	2.5	3.5	2.4	5.7	9.2	4.9
11057	subadult	27.7±	.....	2.6 x ..	5.8	5.3	7.2	4.5	2.95	2.6	3.7	3.0	5.9	8.5±	5.2
11057	subadult	.....	.....	.....	5.7	.....	7.3	4.5	3.00	2.7	3.6	3.0	6.1	9.3±	5.5
11058	young	.....	.....	.....	5.3	5.1	7.5	4.52	3.13	3.0	3.3	2.4	6.2	.....	5.3
11058	young	.....	.....	.....	4.7	(toothless fragment)	.....	.....	.....	.....	.....	.....	.....	.....	.....
8214	subadult	30.7±	7.1	.....	5.4	5.3	7.3	4.5	3.20	2.9	3.7	2.8	5.9	9.0±	5.3±
8165	young	.....	.....	.....	.....	4.7	7.2	4.5	3.30	2.9	3.7	2.8	.....	.....	.....
12045	adult	30.0±	6.7	2.9 x 3.1	6.0	4.7	7.3	4.4	3.10	2.7	3.7	2.7	5.8	8.8	4.8
12046	adult	.....	6.6	2.8 x 2.9	4.7	4.6	7.1	4.38	3.10	2.6	3.5	2.5	5.9	8.9	5.3

with posterior borders of last upper molars; anteroposterior and transverse diameters of M<sub>1</sub> each less than outside length of P<sub>4</sub>; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{1}{2}$ ; infraorbital canal opening above anterior half of P<sub>4</sub>; metaconule of M<sub>1</sub> not distinct; inferior margin of mandible relatively straight; angle about as in *Brachyprotoma* except less globular; step seen in *Mephitis* absent, or less developed (*Spilogale lucasana*); in M<sub>1</sub> trigonid longer than talonid, metaconid high and distinct from protoconid, hypoconid low, entoconid low and separated from protoconid by a wide notch.

*Genotype*—*Mephitis interrupta* Rafinesque.

*Remarks*—Fossil or subfossil remains are known from seven localities and are referable to as many species or subspecies. One is an extinct species but the material from each of the six other localities is referable to the kind living in the same region today.

Probably each of the Recent forms of *Spilogale* occurring within the boundaries of the United States, and now designated as a full species, will be found to intergrade with each of its geographically adjoining species. In that case all the kinds would be arranged as subspecies of a single species. However, since material to prove this for all the species is not available, I have chosen to employ here the name-combinations in current use.

*Spilogale marylandensis* Gidley and Gazin

Plate 5, figs. 2, 2a, 2b

*Spilogale marylandensis* Gidley and Gazin (1933, p. 351, fig. 4).

*Type*—No. 12048, U. S. Nat. Mus.; right mandibular ramus bearing M<sub>1</sub>, P<sub>4</sub>, P<sub>3</sub>, C<sub>1</sub>, the alveoli of M<sub>2</sub> and P<sub>2</sub> but lacking the incisor-bearing portion of the jaw as well as the part posterior to the alveolus of M<sub>2</sub>; from Cumberland Cave, Pleistocene age, 4 miles northwest of Cumberland, Maryland; collected by J. W. Gidley and R. Armbruster in 1914.

*Diagnosis*—"Mandible about the size of that in *Spilogale putorius*. Symphysis abrupt and inferior margin of mandible less convex longitudinally. Canine slender and long. Third and fourth premolars and molar slender and not overlapping. P<sub>3</sub> small. Basal portion of P<sub>4</sub> nearly oval in cross-section as seen in dorsal view. Trigonid of M<sub>1</sub> relatively short and narrow. Metaconid moderately well developed but not so distinctly separated from protoconid as in *S. putorius*. Buccal surface of talonid not offset inwardly to so great an extent as in living species." After Gidley and Gazin (1933, p. 351).

*Remarks*—Comparison of the type specimen of *Spilogale marylandensis* with specimens of *Spilogale putorius*, and the forms bearing the specific or subspecific names *interrupta*, *tenuis*, *gracilis*, *saxatilis*, *olympica*, *latifrons*, *phenax*, *microrhina*, *arizonæ*, *leucoparia*, *ambigua*, *martirensis*, *microdon* and *lucasana*, reveals no Recent specimen closely resembling the fossil. One specimen of *Spilogale leucoparia*, No. 50255, Mus. Vert. Zool., from Malpais Spring, Otero County, New Mexico, has the relative lengths of the trigonid and talonid of M<sub>1</sub> about the same as in *marylandensis* but in other features shows no greater similarity to the fossil than do specimens of *Spilogale putorius* (see Gidley and Gazin, 1933, p. 351).

My own measurements of the breadth of the trigonid and talonid of M<sub>1</sub> of the fossil are in each instance 3.2 mm. and that of the greatest transverse diameter of P<sub>4</sub> is 2.2 mm. Otherwise my measurements agree precisely with those in the original description, to which the reader is also referred for



a detailed comparison with *S. putorius*. It may be added that my own comparison of *S. marylandensis* and *S. putorius*, employing specimens of the latter not seen by Gidley and Gazin, verifies the existence of every comparative difference mentioned by these writers in the original description.

As pointed out by the original describers, *Spilogale marylandensis* appears to be no more closely related to *Brachyprotoma* than are other species of *Spilogale*. Indeed, it is less like *Brachyprotoma* than are the Recent species of *Spilogale*. Basis for this statement is found in the less crowded and narrower premolars in comparison with those in living species of *Spilogale*. Just the opposite conditions exist in *Brachyprotoma*. Also, in *MI* the internal margin is more nearly straight and there is no marked indentation on the lateral border between the protoconid and hypoconid. These irregularities in outline of *MI* are as much, if not more, pronounced in *Brachyprotoma* than in Recent species of *Spilogale*. This more regular lateral outline of *MI*, as seen in occlusal view, is correlated with the fact that the talonid is not offset inward from the trigonid as far as it is in *Brachyprotoma* and in Recent species of *Spilogale*.

#### *Spilogale putorius* (Linnæus)

*Galera perdicida* Cope (1869A, p. 177, pl. 3, figs. 1, 1a); Leidy (1869, p. 445); Coues (1877, p. 16); Schlosser (1899, p. 360).

*G.[alictis] perdicida*, Zittel (1893, p. 650).

*Hemiacis perdicida* Cope (1869B, p. 3, *nomen nudum*).

*Mephitis perdicida*, Schlosser (1888, p. 162); Zittel (1893, p. 652).

*Mephitis putorius*, Cope (1896, p. 387).

*Spilogale perdicida*, Trouessart (1898, p. 262); Hay (1902, p. 766); Trouessart (1904, p. 196).

*Spilogale putorius*, Hay (1923, p. 353; 1930, p. 534).

*Remarks*—Each of the above citations refers to a single specimen, a left mandibular ramus with complete dentition, found by Edward Drinker Cope in a cave deposit in Wythe County, Virginia. Published mention of the specimen first was made under the name *Hemiacis perdicida* by Cope (1869B, p. 3). This constitutes a *nomen nudum*. In the same year (1869A, p. 177, pl. 3, figs. 1, 1a) Cope gave a good description of the specimen under the name "*Galera perdicida* Cope, sp. nov." This constitutes the original description.

In his work entitled "Fur-bearing Animals" Coues (1877, pp. 19, 20) questioned the distinctness of this species from *Spilogale putorius* and in a footnote (*op. cit.*, p. 20) says that in reply to a query of his, Cope, himself, inclined to the same opinion. Later (1896, p. 387) Cope wrote that: "Dr. Coues has suggested that the species was founded on a specimen of *Mephitis putorius*, and on reëxamination of the specimen I am inclined to believe that he is correct."

The present writer has not examined the specimen but, from a study of Cope's description and more especially good figures (1869, pl. 3, figs. 1, 1a), also regards the specimen as of the species of the little spotted skunk living in the region today, *Spilogale putorius*.

So far as known this is the only instance in which *Spilogale putorius* has been found in Pleistocene deposits. Hay's record (1923, p. 322) of *Spilogale putorius* from a cave at Frankstown, Pennsylvania, was on the basis of a manuscript list furnished by Peterson. However, Peterson did not record any species of *Spilogale* from the cave deposit in question when he later (1926) reported on the fauna as a whole. Thus doubt is cast on

this occurrence. The present writer presumes that in preparing the manuscript list for Hay, Peterson misidentified specimen No. 11053, Carnegie Museum, *Brachyprotoma obtusata*, as *Spilogale putorius*. No. 11053 was so misidentified by the present writer at first glance. Its unworn teeth, which are just emerging, show greater resemblance to those of *Spilogale* than do the teeth in adult specimens of *Brachyprotoma*.

*Spilogale ambarvalis* Bangs

*Spilogale ambarvalis*, Hay (1930, p. 534).

*Remarks*—Hay (1930, p. 534) records: "Specimen in U. S. Nat. Mus., from Vero, St. Lucie County, Florida," without further comment. The present writer, in 1930, examined a left lower jaw bearing M1 and the three lower premolars in the United States National Museum which, assumedly, is the specimen referred to by Hay (*loc. cit.*). This specimen, No. 10274, U. S. Nat. Mus., is labeled as from No. 3, Vero, Florida. The specimen has not been critically studied by me.

*Spilogale interrupta* (Rafinesque)

*Spilogale interrupta*, Brown (1908, p. 176); Hay (1914, p. 32; 1924, p. 252; 1930, p. 534).

*Remarks*—This form has been recorded from the Conard Fissure of Arkansas by Brown (1908, p. 176) who speaks of the material as follows: "Two upper teeth, No. 12427, represent this genus and are referred to this species. The outer posterior projecting heel of m1 is strongly developed and the internal cingulum moderately so. Premolar 4 as in recent specimens of this species." So far as known no other material referred to this species has been reported from the Pleistocene. The Conard Fissure material has not been examined by the present writer.

*Spilogale leucoparia* Merriam

*Remarks*—Through the courtesy of Professor Chester Stock, I have been able to examine two skulls, one with lower jaws attached, and two other lower jaws of the little spotted skunk from Shelter Cave, Dona Ana County, New Mexico. The skull clearly is one of the two forms, *Spilogale arizonæ* or *Spilogale leucoparia*. The skull with lower jaws attached is smaller than measured skulls of *arizonæ* and agrees with *leucoparia* which occurs in the same region today. Also, the separate lower jaws are not to be distinguished from those of *S. leucoparia*. The material referred to is in the collection of the Los Angeles Museum of History, Science and Art.

*Spilogale phenax microrhina* Hall

*Spilogale* sp., Stock (1925, p. 30).

*Spilogale*, Osborn (1925, p. 531); Stock (1930, p. 38).

*Spilogale* sp. indet., Hay (1927, p. 184; 1930, p. 534 part).

*Spilogale phenax*, Wilson (1933, p. 66).

*Remarks*—Six skulls of *Spilogale* from Rancho La Brea and now preserved in the Los Angeles Museum of History, Science and Art, Nos. 25 to 30, submitted to me for examination by Professor Chester Stock, are conspecific with the species now living along the west coast of California. The form *amphialus*, restricted to the Channel Islands, has cranial characters which distinguish it from the Rancho La Brea material. The six Rancho La Brea specimens, taking age into account and making a tenta-



tive sex determination, fall nearly midway between *microrhina* as represented by a series from San Diego County and *phenax* as represented by a series from the San Francisco Bay region. By a slight margin the lot falls nearer *microrhina*. One more large specimen similar to No. 28, would throw the average nearer *phenax*.

*Spilogale phenax microrhina* is the subspecies of little spotted skunk which occurs in the vicinity of the Rancho La Brea at the present time. However, individuals from that place are not typical of *microrhina* but are intergrades toward the subspecies *phenax*.

Examination of the two skulls from Carpinteria mentioned by Wilson (1933, p. 66) reveals no features certainly distinguishing them from skulls of intergrades between *S. p. phenax* and *S. p. microrhina*. Because selected intergrades referred to *microrhina* do not differ from these fossils and because the fossils come from a place now within the range of *microrhina* they are here tentatively referred to that subspecies.

#### *Spilogale phenax phenax* Merriam

*Spilogale*, n. sp., Sinclair (1903, p. 711; 1904, p. 16); Miller, L. H., (1912, p. 70); Stock (1918, p. 468); Merriam and Stock (1925, p. 10); Stock (1925, p. 113); Hay (1927, p. 215).

*Spilogale* sp. indet., Hay (1930, p. 534, part).

*Remarks*—The above references apply to remains of *Spilogale* from Potter Creek Cave, on the McCloud River, Shasta County, California. The material is preserved in the University of California Museum of Vertebrate Palæontology. One lower jaw, taken from the lower strata of the cave, and up to now referred to as "*Spilogale* n. sp." presents no features by which the writer is able to distinguish it from selected lower jaws of *Spilogale phenax phenax*, the subspecies which lives in the same region today.

Two lower jaws of the right side and one of the left in the collection of vertebrate fossils at the California Institute of Technology from locality number 138, an excavation in the asphalt deposits at McKittrick, Kern County, California, are to me indistinguishable from *S. p. phenax*, the Recent form found also in that region.

#### Genus OSMOTHERIUM Cope

##### Plate 4

Cope, Proc. Acad. Nat. Sci. Philadelphia, 1896, p. 385.

*Diagnosis*—Size as in *Mephitis mephitis occidentalis*; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{3?}{3} \frac{1}{2}$ ; curvature of inferior margin of mandible about as in *Mephitis* but angle (in one specimen where preserved) about as in *Brachyprotoma*, that is to say not expanded so far vertically as in *Mephitis*, or so far horizontally as in *Conepatus*; coronoid process high and in adults vertically inclined; in M1 trigonid longer than talonid, paraconid—protoconid interspace for reception of internal cusp of P4 greatly reduced, metaconid low and appressed to protoconid, hypoconid low, entoconid low and joined to protoconid by a series of one to three cusps forming a ridge on the internal basid of the talonid.

*Genotype*—*Osmotherium spelæum* Cope.

*Remarks*—This genus is known only from the Port Kennedy bone deposit of Pleistocene age in Montgomery County, Pennsylvania. From this de-



posit Cope states (1899, p. 232) that he examined ". . . at least fifty-five individuals" of the form here designated as *Osmotherium spelæum*. However, Cope recognized in this material five species which he referred to three genera. As basis for reducing to synonymy four of these five species I have relied principally upon my own examination of the type specimens of these species. The type specimens of all save that of *Pelycictis lobulatus* have been available for study, and some additional material, as listed in the table of measurements of *Osmotherium*, also has been seen.

Cope's (1899, p. 232) suggestion that fragments of two upper jaws from the Port Kennedy bone deposit could not be distinguished from the existing *Mephitis* indicates that *Osmotherium* and *Mephitis* may have been contemporaneous though we can not be certain on this point.

In addition to the statement of structural features of *Osmotherium* as given above under "*Diagnosis*," it may be mentioned that, on the average, in comparison with *Mephitis mephitis occidentalis*, the talonid is longer relative to the trigonid and the total length of M1 and P4 is greater.

The construction of the medial side of the talonid of M1 is markedly different in the two genera, *Mephitis* and *Osmotherium*. In the latter the basin of the talonid is shallower. The entoconid is lower but usually is carried anteriorly along the medial side of the tooth farther than in *Mephitis*. Also, there are in *Osmotherium* one to three accessory cusps longitudinally arranged between the bases of the entoconid and protoconid. These cusps form a raised margin on the lingual side of the basin of the talonid. In *Mephitis* these cusps between the entoconid and protoconid are absent, or in freshly emerged teeth are represented by only a single, small cusp. In either case there is no raised margin on the lingual side of the basin of the talonid of M1, but instead a deep notch leading out from the basin of the talonid through the lingual side of the tooth between the protoconid and entoconid. As implied in the above description and as may be seen from the figures on Plate 4, the entoconid in *Mephitis*, although higher than in *Osmotherium*, usually is not carried so far forward along the lingual side of the tooth.

In M1 the low entoconid and hypoconid, the smaller metaconid and the reduced paraconid-protoconid interspace for reception of the internal cusp of P4 are features seen in more or less degree in *Brachyprotoma*. The shorter talonid, size of M2, general size of lower jaw, less crowded premolars and dental formula in the lower jaw, agree with characters seen in *Mephitis*. From these resemblances and other features of structure as shown in the figures, *Osmotherium* is judged to be more closely related to *Mephitis* than to any other known genus of the Mephitinæ.

#### *Osmotherium spelæum* Cope

##### Plate 4

*Osmotherium spelæum* Cope (1896, p. 385); Trouessart (1898, p. 260); Cope (1899, p. 230, pl. 18, fig. 6); Schlosser (1899, p. 362; 1902, p. 141); Hay (1902, p. 766); Rhoads (1903, p. 230); Trouessart (1904, p. 191); Baker (1920, pp. 208, 214, 397); Hay (1923, p. 312; 1930, p. 532).

*Brachyprotoma fossidens*, Brown (1908, p. 176); Hay (1930, p. 531).

*Brachyprotoma leptops*, Brown (1908, p. 177); Hay (1930, p. 532).

*Mephitis fossidens* Cope (1896, p. 386); Trouessart (1898, p. 259); Cope (1899, p. 230, pl. 18, fig. 7); Howell (1901, p. 16); Schlosser (1902, p. 142); Hay (1902, p. 766); Rhoads (1903, p. 230); Trouessart (1904, p. 192); Baker (1920, pp. 208, 214, 397); Hay (1923, p. 312).

*Mephitis fodiens* Schlosser (1899, p. 360), obviously a *lapsus calami* for *Mephitis fossidens* Cope.

- Mephitis leptops* Cope (1899, p. 235, pl. 8, figs. 9, 9a); Howell (1901, p. 17); Hay (1902, p. 766); Schlosser (1902, p. 142); Rhoads (1903, p. 230); Trouessart (1904, p. 192); Baker (1920, pp. 208, 215, 397); Hay (1923, p. 312).
- Mephitis mephitica*, Cope (1895, p. 447).
- Mephitis orthostichus* Cope (1896, p. 389); Trouessart (1898, p. 259); Schlosser (1899, p. 360); Cope (1899, p. 234, pl. 18, figs. 8, 8a); Howell (1901, p. 19); Schlosser (1902, p. 142); Rhoads (1903, p. 230); Baker (1920, pp. 208, 215, 397).
- Mephitis orthostica*, Hay (1902, p. 766).
- Mephitis orthostica*, Hay (1923, p. 312; 1930, p. 533).
- Pelycietis lobulatus* Cope (1896, p. 390); Trouessart (1898, p. 261); Cope (1899, p. 237, pl. 18, fig. 10, and 1 text fig.); Schlosser (1899, p. 362; 1902, p. 142); Hay (1902, p. 766); Rhoads (1903, p. 231); Trouessart (1904, p. 191); Baker (1920, pp. 208, 214, 397); Hay (1923, p. 312; 1930, p. 533).

*Type*—No. 67, Academy of Natural Sciences of Philadelphia; right mandibular ramus (see figures 2, a, b, of Plate 4) bearing  $M\bar{2}$ ,  $M\bar{I}$ ,  $P\bar{4}$ , roots of  $P\bar{3}$ , the alveoli of  $P\bar{2}$ , and part of the alveolus of the canine; from the Port Kennedy bone deposit (Pleistocene age), right bank of Schuylkill River, two miles below Valley Forge, Upper Merion Township, Montgomery County, Pennsylvania.

*Referred specimens*—Twelve lower jaws from the same place as the type and preserved in the Academy of Natural Sciences of Philadelphia. For detailed list of specimens examined by the writer see table of measurements.

*Diagnosis*—A single species known to which, therefore, characters as given for the genus may be applied.

*Remarks*—According to Cope (1896, p. 385; 1899, p. 230) *Osmotherium* differed from *Mephitis* in possessing a first (= fourth in Cope's terminology) premolar and in having a deeper horizontal mandibular ramus, the lower border of which first began to incline upward below  $M\bar{I}$  instead of below  $M\bar{2}$  as in *Mephitis*. The differences in depth and curvature of the ramus are well within the bounds of variation to be seen in a series of specimens of *Mephitis* of a single subspecies from one locality. As regards the dental formula, the type-specimen shows the two roots of  $P\bar{4}$ , the two alveoli of  $P\bar{3}$ , two alveoli of  $P\bar{2}$ , a number which occurs in many specimens of *Mephitis*, and a small indentation at the posterior margin of the alveolus of the canine. This indentation had been probed and a minute, alveolar-like cavity was thereby made into the calcified matrix which filled the alveolus of the canine. Application of a minute amount of water on the area in question brought the two substances, bone and matrix, into clear and contrasting relief, permitted a clearing away of the matrix, and showed the supposed alveolus to be, instead, merely a hiatus where a portion of the posterior margin of the alveolus of the canine had broken out. Thus little, if any, doubt remains that, contrary to Cope's belief, only three premolars were present in the lower jaw. No characters of systematic worth which would separate the specimen from others in the same deposit have been found. There was, therefore, good reason for Cope's (1896, p. 386) note of skepticism relative to the distinctness of this species in his closing remark concerning it. Cope (*loc. cit.*) said: "The only question as to the validity of this form that can arise, is due to its similarity to *Mephitis fossidens*." Indeed, *Osmotherium spelæum* is conspecific with the subsequently named forms *Mephitis fossidens*, *Mephitis orthostichus*, *Mephitis leptops*, and probably, also, as will be set forth later, with *Pelycietis lobulatus*.

Without recounting in detail the reasons for regarding each of the differential features found, and those mentioned by Cope, in *M. fossidens*, *M. orthostichus* and *M. leptops*, as not of systematic worth, it may be mentioned that in a series of only thirty-seven individuals of the single sub-



species *Mephitis mephitis occidentalis* there exist variations in actual size of and relative proportions of parts measured, which, in range, as determined by computing the per cent of variation from the maximum in any given measurement, in each case equals or exceeds the percentage of variation encountered in material representing Cope's five alleged species from the Port Kennedy bone deposit. The form *M. m. occidentalis*, rather than *M. m. mephitis* which now occurs in the region of Port Kennedy, was employed for a determination of range of variation because more specimens of *occidentalis* happened to be available for study.

In some cases Cope relied on differences due to age (ontogenetic stage of the individual) to distinguish one species from the other. This was true of *M. leptops* where, also, failure to correctly determine the amount lacking

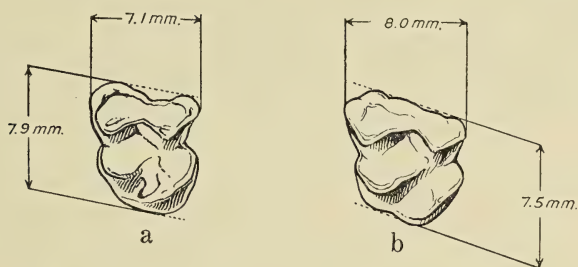


FIG. 3—Occlusal views of two left upper molars of *Mephitis mephitis occidentalis* Baird to show expectable variation, within a single subspecies, in proportion of breadth to length.

- a. Young female, No. 23669, Mus. Vert. Zool.; Chin-quapin, Yosemite National Park, California.
- b. Subadult male, No. 21138, Mus. Vert. Zool.; Car-lotta, Humboldt County, California.

in the posterior part of the horizontal ramus led him to an erroneous conclusion regarding the shape of the post-molar part of the jaw. In other instances Cope utilized differences resulting from individual and secondary sexual variation. Certainly this was true of characters in the inferior dentition and lower jaws and it appears to have been true of his treatment (1896, p. 386; 1899, p. 232) of M1. Unfortunately I have not been able to examine any of the upper teeth from the Port Kennedy deposit. However, the differences in M1 described by Cope as existing between *Mephitis fossidens* and *Mephitis orthostichus* are no greater in degree than those found between individuals of the same subspecies of Recent *M. m. occidentalis*.

The differing shape of the eminence or eminences resulting from development of the lateral cusps of M1, as described by Cope, is not of greater degree than that found in Recent *M. m. occidentalis*. Also, the proportion of breadth to length in M1 shows a variation of 19 per cent which is but 1 per cent more than in two specimens before me of *M. m. occidentalis* (see fig. 3). In addition, one may doubt the accuracy of Cope's measurements of these upper molars because his measurements of the teeth in the lower jaw were found to be subject to as much as 10 per cent correction from the mean. Also there is question as to whether or not the different teeth were measured by Cope in exactly the same way (see Cope, 1899, pp. 233 and 235).

Brown (1908, pp. 176-177) placed *Mephitis fossidens* Cope and *Mephitis leptops* Cope in his new and distinct genus *Brachyprotoma*. Probabilities



are that Brown was misled by that part of Cope's description which characterized these two species as having: the premolar-bearing part of the lower jaw short, relative to the molar-bearing part; premolars crowded and placed more or less transversely; M1 relatively short (anteroposteriorly), and other structural features which, as described, agree well enough with those of the genus *Brachyprotoma*. However, examination of the specimens themselves shows that they are not at all *Brachyprotoma* although they do approach that genus a little more closely than does *Mephitis*. Also, as may be deduced from a comparison of text-figure 3 with figures 3 and 6 of Plate 2, Cope's published measurements (8.0 mm.  $\times$  9.5 mm.) of *M. fossidens* do not necessarily indicate the type of tooth found in *Brachyprotoma*. The shortening of the premolar part of the jaw alluded to by Cope in the two species in question is not carried to the extreme found in *Brachyprotoma*. Indeed, the shortening is little, if any, more than that in *Mephitis*. Even in *Mephitis* the combined lengths of the premolars may be more or less than the length of M1. Extremes in this regard, as shown in the table of measurements on page 63, are furnished by No. 24827 in which M1 is 1.5 mm. longer than the crown length of the premolars and by No. 12898 in which M1 is 1.1 mm. shorter than the crown length of the premolars.

*Pelycictis lobulatus* Cope is known to me only from published description and figures. The type specimen could not be found in 1930 when search was made for it in the Academy of Natural Sciences of Philadelphia. The distinguishing feature of this genus and species according to Cope (1896, pp. 390-391; 1899, pp. 237, 238, pl. 18, fig. 10, and 2 text-figs.) is the combination of a basined talonid with a trigonid on which the metaconid is absent. Careful study of the description and figures clearly shows that the specimen bears no close relation to *Martes americana*, *Mustela vison*, or other known genera save *Osmotherium* and *Mephitis*. Indeed, this comparison reveals no character by which the specimen can be distinguished from other specimens of *Osmotherium spelæum* from the Port Kennedy bone deposit, save for the alleged absence of the metaconid. On the same page (1899, p. 237) where the metaconid is stated to be absent, Cope writes "The metaconid of the sectorial is represented by a convexity of the internal edge of the protocone." The text-figures on page 237 (*op. cit.*) definitely show a metaconid. Figure 10 of plate 18 (*op. cit.*), though hazy in the region of the metaconid, also shows what seems to be a metaconid. Perhaps the metaconid was relatively low but it almost certainly was not absent in the sense that it is absent in *Felis* or in *Mustela*. Cope's (1899, p. 238) measurements record the length of M1 as 8.5 whereas on figure 10 (*op. cit.*), which seems to be natural size, the tooth is represented as 9.5 mm. in length. This discrepancy is not unique. For instance Cope's measurements (*op. cit.*) of the length of M1 in the type specimens of *M. leptops* and *Osmotherium spelæum* are in each case given as 10.0 mm., whereas from the same specimens I obtain a measurement of 11.1 mm. for *O. spelæum* and one of only 9.5 mm. for *M. leptops*. The point to be emphasized is that M1 of *Pelycictis lobulatus* is not smaller than that of some specimens of *Osmotherium spelæum* from the same deposit. In summary: *Pelycictis lobulatus* is thought to be a synonym of *Osmotherium spelæum*.

#### Genus MEPHITIS Geoffroy and Cuvier

Geoffroy and Cuvier, Mag. Encyclop., 1<sup>re</sup> année, vol. 2, p. 187. 1795.

*Diagnosis*—Skull ranging from 56 to 76 mm. in basal length; highly arched and deepest in frontal region; mastoid bullæ not inflated; posterior margin

*Mephitis mephitis occidentalis*, from California, for comparison with corresponding measurements of available specimens of *Osmotherium spelaeum* from the Port Kennedy bone deposit. The latter probably represent extremes from a series of fifty-five individuals (see Cope, 1899, p. 232). Extremes are italicized.

Sex and age	Catalogue number	Collection	Species (current name)	Greatest length of jaw (lateral end of condyle to anterior border of alveolus of I <sub>1</sub> )	Depth of jaw at posterior border of canine	Depth of jaw at anterior border of M <sub>1</sub>	Depth of jaw at posterior border of M <sub>1</sub>	Greatest length of M <sub>1</sub>	Width of M <sub>1</sub> through base of metaconid	Least width of talonid	Outside length of P <sub>4</sub>	Crown lengths not alveolar lengths		
												P <sub>4</sub> to P <sub>2</sub> inclusive	P <sub>4</sub> to anterior-most part of canine	P <sub>4</sub> to P <sub>3</sub> and P <sub>3</sub>
♂ ad.	12897	M.V.Z.	<i>Mephitis m. occidentalis</i>	53.6	11.1	8.7	8.8	10.4	4.4	4.5	4.6	11.7	18.0	8.6
♂ ad.	21135	M.V.Z.	"	52.8	10.7	8.8	9.5	10.6	4.4	4.6	4.6	11.4	16.9	8.4
♂ yg.	4932	M.V.Z.	"	52.8	10.5	7.5	8.6	10.6	4.4	4.3	4.8	10.7	17.0	8.8
♀ ?ad.	4978	M.V.Z.	"	49.5	10.6	8.0	8.5	10.5	4.6	4.8	4.4	10.8	16.2	8.0
♂ yg.	19738	M.V.Z.	"	51.3	10.7	7.5	8.2	10.7	4.3	4.7	4.5	11.3	17.1	8.2
♂ ad.	12898	M.V.Z.	"	49.7	11.0	8.9	10.1	9.6	3.9	3.9	4.3	10.7	16.2	8.0
♀ ad.	11742	M.V.Z.	"	48.1	11.8	7.9	9.0	9.8	4.2	4.2	4.2	10.7	15.7	7.9
♀ ?ad.	24827	M.V.Z.	"	46.4	9.9	8.0	8.6	10.1	4.3	4.4	4.0	8.6	13.6	6.8
♂ yg.	19733	M.V.Z.	"	36.4	7.0	5.0	5.8	9.9	4.0	3.8	4.2	8.9	11.2	7.1
♀ yg.	28067	M.V.Z.	"	39.8	7.1	5.9	6.3	9.6	3.9	3.8	3.8	12.3	12.3	7.0
♂ ad.	23694	M.V.Z.	"	48.1	10.0	7.8	8.9	9.5	3.77	3.5	4.5	10.5	15.8	8.0
♂ yg.	18478	M.V.Z.	"	40.6	7.0	5.7	7.3	9.1	3.8	3.7	.....	.....	.....	.....
ad.	67	A.N.S. Phila.	(Cope's names)	.....	.....	8.8	9.4	11.1	4.9	5.0	4.9	.....	.....	.....
ad.	68	A.N.S. Phila.	<i>Osmotherium spelaeum</i> (type)	.....	.....	8.0	8.5	11.2	5.05	4.95	5.0	.....	14.9	8.5
ad.	69	A.N.S. Phila.	<i>Mephitis fossidens</i>	.....	.....	7.6	8.3	10.7	4.6	4.3	.....	.....	.....	.....
ad.	69	A.N.S. Phila.	" (type)	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
			" (edentulous, save P <sub>4</sub> and pathologic)	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
yg.	70	A.N.S. Phila.	<i>Mephitis fossidens</i>	.....	.....	7.3	7.7	10.85	.....	.....	4.8	.....	.....	.....
sad.	72	A.N.S. Phila.	no name	.....	.....	8.2	.....	10.6	5.0	4.6	4.8	.....	14.3±	8.0±
yg.	71	A.N.S. Phila.	<i>Mephitis orthostichus</i> (type)	.....	.....	.....	.....	9.5	4.5	4.3	4.6	.....	.....	8.5
ad.	73	A.N.S. Phila.	"	44.3	10.2	8.2	8.7	10.0	4.6	4.2	4.3	11.2±	.....	7.8
yg.	75	A.N.S. Phila.	<i>Mephitis leptops</i>	.....	.....	6.1	7.0	9.5	4.2	4.1	4.0	9.25	.....	.....
yg.	75	A.N.S. Phila.	" (edentulous type)	.....	.....	7.1	7.5	10.4±	.....	.....	.....	.....	.....	.....
ad.	76	A.N.S. Phila.	no name	.....	.....	.....	.....	10.7	.....	.....	.....	.....	.....	.....
yg.	80	A.N.S. Phila.	no name	.....	.....	7.3	7.0	10.3	4.5	.....	4.1	.....	.....	.....
Per cent of variation from maximum in fossils.....				32	41	31	25	15	16	18	20	17	4	8
Per cent of variation from maximum in Recent specimens.....				.....	.....	44	43	15	18	27	21	24	38	23



of palate nearly on a line with posterior borders of upper molars; antero-posterior and transverse diameters of  $M_1$  each about equal to (usually more than) outside length of  $P_4$ ; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{1}{2}$ ; infraorbital canal opening above posterior half of  $P_4$ ; metaconule of  $M_1$  not distinct; inferior margin of mandible curved; angle of mandible developed as flattened face in a vertical plane producing a "step" or concavity in the inferior margin; coronoid process high and vertically inclined; in  $M_1$  trigonid longer than talonid, metaconid high and distinct from protoconid, hypoconid high, entoconid high and separated from protoconid by deep, wide notch.

*Genotype*—*Viverra mephitis* Schreber.

*Remarks*—Recent North American skunks of the genus *Mephitis*, in the writer's opinion, are representative of only two species. These are *Mephitis mephitis* (Schreber) which comprises the subgenus *Mephitis*, and *Mephitis macroura* Lichtenstein which comprises the subgenus *Leucomitra* Howell (1901, p. 38). Although Howell (1901) recognized several distinct species when he revised the group, much additional material has been accumulated since his study was made. Some of this additional material clearly shows intergradation between forms previously regarded as full species and suggests that the same state of affairs exists between all of the geographically adjacent races of the subgenus *Mephitis*.

Howell, himself, since writing his monograph (*op. cit.*), seems to have come to the same conclusion. At any rate, in his treatment of the mammals of Alabama (1921, p. 39), the forms *elongata* and *nigra* are listed as subspecies of *Mephitis mephitis*. The forms commonly arranged as subspecies of *Mephitis mesomelas* namely, *avia* and *varians*, recently have been connected with the species heretofore known as *Mephitis estor*, by Bailey (1931, p. 333) who comments on intergradation as between *varians* and *estor* in Arizona. The same relation has been commented on by Hall (1931, p. 1) with respect to material from southeastern Utah. Specimens in the Museum of Vertebrate Zoology from southeastern California and northeastern Lower California show intergradation between *estor* and the currently designated *Mephitis occidentalis holzneri* Mearns. The subspecies *holzneri*, since Howell's revision (*op. cit.*), has been regarded as one form of the intergrading series, *occidentalis*, *major*, *notata*, and *spissigrada*. Material recently acquired from British Columbia by the Museum of Vertebrate Zoology indicates that intergradation occurs there between *spissigrada* and *Mephitis americana* var. *hudsonica* Richardson.

Therefore, evidence of some weight, if not of ideal clarity, is available to show that the several forms mentioned above, should, on the criterion of intergradation, be arranged as subspecies of the single species *Mephitis mephitis* (Schreber).

As best expressing our present state of knowledge concerning this group of named forms, the following list is suggested as an arrangement approximating correctness more closely than the one currently employed.

*Mephitis mephitis mephitis* (Schreber).

- 1776. *Viverra mephitis* Schreber, Säugthiere, pl. 121. 1776.
- 1792. *Viverra mephitica* Shaw, Museum Leverianum, p. 171. 1792.
- 1818. *Mephitis americana* Desmarest, Nouv. Dict. d'Hist. Nat., Paris xxi, p. 514. 1818.
- 1842. *Mephitis vulgaris* Cuvier, Hist. Nat. Mamm. vii, Table Gen. et Method, p. 3. 1842.
- 1901. *Chincha mephitis*, Howell, North Amer. Fauna, No. 20, p. 22. August 31, 1901.
- 1902. *Mephitis mephitis*, Allen and others, Science, n. s., vol. 16, p. 115. July 18, 1902.



*Type Locality*—Eastern Canada.

*Range*—Eastern Canada: Nova Scotia, Quebec, and northern Ontario; west and north at least to Oxford House, Keewatin.

*Mephitis mephitis hudsonica* Richardson.

1829. *Mephitis americana* var. *hudsonica* Richardson, Fauna Boreali—Americana, vol. 1, p. 55. 1829.  
 1895. *Mephitis hudsonica*, Bangs, Proc. Boston Soc. Nat. Hist., vol. 26, p. 536. July 31, 1895.  
 1901. *Chincha hudsonica*, Howell, North Amer. Fauna, No. 20, p. 24. August 31, 1901.  
 1911. *Mephitis minnesotæ* Brass, Aus dem Reiche der Pelze, p. 532. April, 1911.

*Type Locality*—Plains of the Saskatchewan, Canada.

*Range*—Western Canada from Manitoba to British Columbia (through the Cascades); south in the United States to Nebraska and northern New Mexico.

*Mephitis mephitis nigra* (Peale and Beauvois).

1796. *Viverra nigra* Peale and Beauvois, Catl. Peale's Mus., Philadelphia, p. 37, 1796.  
 1842. *Mephitis putida* Boitard, Jardin des Plantes, Mamm., p. 147. 1842.  
 1875. *Mephitis frontata* Coues, Bull. No. 1, U. S. Geol. and Geogr. Surv. Territories, p. 7, fig. 1. 1875.  
 1885. *Mephitis mephitica*, True, Proc. U. S. Nat. Mus., vol. 7 (1884), p. 609. 1885 (Part).  
 1901. *Chincha putida*, Howell, North Amer. Fauna, No. 20, p. 25. August 31, 1901.  
 1911. *Mephitis nigra*, Hollister, Proc. Biol. Soc. Washington, vol. 27, p. 215. October 31, 1914.  
 1921. *Mephitis mephitis nigra*, Howell, North Amer. Fauna, No. 45, p. 39. October 28, 1921.

*Type Locality*—Maryland.

*Range*—New England, southern Ontario, and Middle Atlantic States; south to Alabama; west to Indiana.

*Mephitis mephitis elongata* Bangs.

1895. *Mephitis mephitis elongata* Bangs, Proc. Boston Soc. Nat. Hist., vol. 26, p. 531. July 31, 1895.  
 1901. *Chincha elongata*, Howell, North Amer. Fauna, No. 20, p. 27. August 31, 1901.  
 1921. *Mephitis mephitis elongata*, Howell, North Amer. Fauna, No. 45, p. 39. October 28, 1921.

*Type Locality*—Micco, Brevard County, Florida.

*Range*—Florida (from vicinity of Lake Worth) to North Carolina; westward through Georgia, southern half of Alabama to the Mississippi River on the coast.

*Mephitis mephitis avia* Bangs.

1898. *Mephitis avia* Bangs, Proc. Biol. Soc. Washington, vol. 12, p. 32. March 24, 1898.  
 1901. *Chincha mesomelas avia*, Howell, North Amer. Fauna, No. 20, p. 30. August 31, 1901.  
 1908. *Mephitis mephitica newtonensis* Brown, Mem. Amer. Mus. Nat. Hist., vol. 9, pt. 4, p. 175, pl. 16. 1908.

*Type Locality*—San Jose, Mason County, Illinois.

*Range*—Prairie region of Illinois, western Indiana, eastern Iowa, northern Missouri, eastern Kansas; boundaries of range imperfectly known.

*Mephitis mephitis mesomelas* Lichtenstein.

1832. *Mephitis mesomelas* Lichtenstein, Darstellung neuer oder wenig bekannter Säugethiere, pl. 45, fig. 2. 1832.  
 1896. *Mephitis mephitica scrutator* Bangs, Proc. Biol. Soc. Washington, vol. 10, p. 141. December 28, 1896.  
 1901. *Chincha mesomelas*, Howell, North Amer. Fauna, No. 20, p. 29. August 31, 1901.

*Type Locality*—Louisiana.

*Range*—West side of Mississippi Valley from southern Louisiana to Missouri; westward along the coast of Texas to Matagordo Island; and up the Red River Valley as far at least as Wichita Falls.

*Mephitis mephitis varians* Gray.

1837. *Mephitis varians* Gray, Charlesworth's Mag. Nat. Hist., vol. 1, p. 581. 1837.  
 1901. *Chincha mesomelas varians*, Howell, North Amer. Fauna, No. 20, p. 31. August 31, 1901.

*Type Locality*—Texas.

*Range*—Southern and western Texas, eastern two-thirds of New Mexico and adjacent parts of Mexico; northward into Oklahoma, Colorado, Kansas and Nebraska.

*Mephitis mephitis estor* Merriam.

1890. *Mephitis estor* Merriam, North Amer. Fauna, No. 3, p. 81. September 11, 1890.  
 1901. *Chincha estor*, Howell, North Amer. Fauna, No. 20, p. 32. August 31, 1901.  
 1931. *Mephitis mephitis estor*, Hall, Univ. Calif. Publ. Zool., vol. 37, p. 1. April 10, 1931.

*Type Locality*—San Francisco Mountain, Arizona.

*Range*—Western third of New Mexico across Arizona to northeastern Lower California and the Colorado River Valley of California; southward in Sonora, and in the Sierra Madre to southern Chihuahua; limits of range unknown.

*Mephitis mephitis major* (Howell).

1901. *Chincha occidentalis major* Howell, North Amer. Fauna, No. 20, p. 37. August 31, 1901.  
 1931. *Mephitis mephitis major*, Hall, Univ. Calif. Publ. Zool., vol. 37, p. 2. April 10, 1931.

*Type Locality*—Fort Klamath, Klamath County, Oregon.

*Range*—Eastern Oregon, southeastern Idaho south to the Colorado River; eastward to the Wasatch Mountains, Utah; westward to the Sierra Nevada, Owens Valley and Northeastern California.

*Mephitis mephitis holzneri* Mearns.

1897. *Mephitis occidentalis holzneri* Mearns, Preliminary diagnosis of new mammals of the genera Lynx, Urocyon, Spilogale, and Mephitis, from the Mexican boundary line, p. 4. January 12, 1897. (Reprint: Proc. U. S. Nat. Mus., vol. 20, p. 461. December 24, 1897.)  
 1901. *Chincha occidentalis holzneri*, Howell, North Amer. Fauna, No. 20, p. 38. August 31, 1901.

*Type Locality*—San Isidro Ranch, Lower California, Mexico, near border of San Diego County, California.

*Range*—Southern California from Monterey Bay southward in the Coast Range and along the coast to mouth of Santa Domingo River, Lower California.

***Mephitis mephitis occidentalis* Baird.**

1857. *Mephitis occidentalis* Baird, Mamm. N. Amer., p. 194. 1857.  
 1901. *Chincha occidentalis*, Howell, North Amer. Fauna, No. 20, p. 34. August 31, 1901.  
 1901. *Chincha platyrhina* Howell, North Amer. Fauna, No. 20, p. 39. August 31, 1901.

*Type Locality*—Petaluma, Sonoma County, California.

*Range*—Northern and central California, from Monterey Bay northward, west of the Sierra Nevada and Cascades, to the Willamette Valley, Oregon.

***Mephitis mephitis notata* (Howell).**

1901. *Chincha occidentalis notata* Howell, North Amer. Fauna, No. 20, p. 36. August 31, 1901.

*Type Locality*—Trout Lake, Mount Adams, Washington.

*Range*—Southern Washington and northern Oregon, east of the Cascades; exact limits of range unknown.

***Mephitis mephitis spissigrada* Bangs.**

1898. *Mephitis spissigrada* Bangs, Proc. Biol. Soc. Washington, vol. 12, p. 31. March 24, 1898.  
 1899. *Mephitis foetulenta* Elliot, Field Columb. Mus., pub. 32, Zool., ser., vol. 1, p. 269. March, 1899.  
 1901. *Chincha occidentalis spissigrada*, Howell, North Amer. Fauna, No. 20, p. 35. August 31, 1901.

*Type Locality*—Sumas, British Columbia.

*Range*—Shores of Puget Sound and coastal region of Washington and northern Oregon.

***Mephitis macroura macroura* Lichtenstein.**

1832. *Mephitis macroura* Lichtenstein, Darstellung neuer oder wenig bekannter Säugethiere, pl. 46. 1832.  
 1861. *Mephitis longicaudata* Tomes, Proc. Zool. Soc. London, 1861, p. 280. 1861.  
 1877. *Mephitis edulis* Coues, Fur-bearing Animals, p. 236. 1877.  
 1901. *Chincha macroura*, Howell, North Amer. Fauna, No. 20, p. 41. August 31, 1901.

*Type Locality*—Mountains northwest of the City of Mexico.

*Range*—Highlands of central and southern Mexico, south to Guatemala.

***Mephitis macroura milleri* Mearns.**

1897. *Mephitis milleri* Mearns, Preliminary diagnoses of new mammals of the genera *Mephitis*, *Dorcelaphus*, and *Dicotyles*, from the Mexican boundary of the United States, p. 1. February 11, 1897. (Reprint: Proc. U. S. Nat. Mus., vol. 20, p. 467. December 24, 1897.)  
 1901. *Chincha macroura milleri*, Howell, North Amer. Fauna, No. 20, p. 42. August 31, 1901.  
 1901. *Mephitis macroura milleri*, Allen, Bull. Amer. Mus. Nat. Hist., vol. 14, p. 334. November 12, 1901.

*Type Locality*—Fort Lowell, near Tucson, Pima County, Arizona.

*Range*—Southern Arizona, Sonora, and parts of Chihuahua, Sinaloa, Durango, and Choahuila.

***Mephitis macroura vittata* Lichtenstein.**

1832. *Mephitis vittata* Lichtenstein, Darstellung neuer oder wenig bekannter Säugethiere, pl. 47. 1832.  
 1865. *Mephitis concolor* Gray, Proc. Zool. Soc. London, 1865, p. 149. 1865.  
 1869. *Mephitis vittata* var. *intermedia* Gray, Catalogue of Carnivorous, Pachydermatous, and Edentate Mammalia in the British Museum, p. 138. 1869.



1901. *Chincha macroura vittata*, Howell, North Amer. Fauna, No. 20, p. 43. August 31, 1901.  
 1901. *Mephitis macroura vittata*, Allen, Bull. Amer. Mus. Nat. Hist., vol. 14, p. 334. November 12, 1901.

*Type Locality*—San Mateo del Mar Oaxaca, Mexico.

*Range*—Known only from the type locality; probably ranges over the coast region of Oaxaca and Chiapas.

The above list is essentially that of Miller (1924, p. 136) with certain changes. Changes from Miller's (*op. cit.*) list, for which reasons have not been given already, may be mentioned as follows:

*Mephitis minnesotæ* Brass on the basis of information available is not found to differ from *Mephitis americana* var. *hudsonica* Richardson as that form now is known.

*Mephitis platyrhina* Howell may, at most, be a valid subspecies. However, examination of the available material indicates that the special characters relied upon by Howell as distinctive of the type specimen of *platyrhina* crop up at various places within the ranges of *M. m. holzneri* Mearns and *M. m. occidentalis* Baird. The average of specimens from the general region of the type-locality is nearest to that of *occidentalis*.

Modifications from Howell's (*op. cit.*) statements of range are made on the basis of personal examination of specimens. Citations to literature dealing with the several generic names applied to the genus now designated as *Mephitis* may be found in Miller (*op. cit.*).

Eight specific names, at one time or another applied to forms of the genus *Mephitis*, thought now to be inapplicable are not cited in the above list. These are *bivirgata*, *cinche*, *fetidissima*, *fæda*, *laticaudata*, *memphitis*, *mexicana* and *olida*. These are dealt with by Howell (1901, pp. 15-19).

With only two species in the genus *Mephitis* there seems to be but little if any need for employing the subgeneric names *Mephitis* and *Leucomitra*.

The habits of *Mephitis*, including the excavating of its own burrows, the occupying of deserted ones of other animals, and the choosing of fissures in the rocks and small caves for winter quarters, would lead one to expect its remains commonly to appear in cave or fissure deposits. This expectation is realized, for this skunk has been found in most of the North American cave deposits of Quaternary age that have yielded fairly large collections of fossil remains. It is absent from Cumberland Cave in Maryland and probably from the Port Kennedy Cave in Pennsylvania. Doubt as to the occurrence of *Mephitis* in the Port Kennedy deposit is felt because Cope (see page 69) did not definitely record it from this accumulation in his final paper treating of the vertebrate assemblage. The forms which he assigned to the genus *Mephitis* in this last paper are now referred to the genera *Brachyprotoma* and *Osmotherium*.

The relative scarcity of remains of *Mephitis* in the Conard Fissure, of Arkansas, coupled with their seeming absence in the Cumberland Cave and Port Kennedy deposits of even earlier age, leaves a question as to whether or not *Mephitis* was present in North American faunas of the earlier Pleistocene stages so far found. In view of the habits of skunks, as mentioned above, it is sometimes difficult to determine whether the remains of these forms in a cave accumulation, as for example that of the Conard Fissure, Arkansas, represent a primary burial or secondary introduction at some later time. However, the frequency of association of *Mephitis* with extinct Pleistocene forms, leaves little if any doubt that *Mephitis* lived in North America during at least the late part of the Pleistocene.

Careful study by the writer of remains of *Mephitis*, regarded up to now as pertaining to extinct species of the genus, has shown in every instance that these are either indistinguishable from Recent species found in that region today or are referable to some other genus. Thus it can be said that no extinct species of *Mephitis*, or even extinct subspecies, has been demonstrated as yet to occur in Pleistocene deposits. Detailed evidence in support of this view will be found below under the discussion of forms to which the fossil or subfossil remains are referred.

*Mephitis mephitis nigra* (Peale and Beauvois)

- Mephitis frontata* Coues (1875, p. 7, fig. 1); anonymous (1876, p. 499); Allen (1876, p. 333); Coues (1877, p. 193); Trouessart (1898, p. 260); Howell (1901, p. 16); Hay (1902, p. 766); Hay (1930, p. 533).  
*Mephitis mephitica*, Allen (1876, p. 333); Leidy (1880, p. 348); Leidy (not seen, 1889, pp. 5, 18); Zittel (1893, p. 652, part); Trouessart (1898, p. 259); Hay (1902, p. 766); Peterson (1926, p. 284, fig. 6).  
*Mephitis nigra*, Hay (1930, p. 533).  
*Mephitis putida*, Trouessart (1904, p. 192, part); Hay (1923, pp. 310, 311).  
*Mephitis mephitis putida*, Rhoads (1903, p. 230).  
*Mephitis* sp. indet., Hay (1923, p. 321).  
 "Skunk," Leidy (1880, p. 349).

*Remarks*—The above synonymy refers strictly to materials regarded by one or another writer as of Pleistocene age. Reference by Cope (1895, p. 447) and by Schlosser (1899, p. 360) to *Mephitis mephitica* and by Hay (1923, p. 312) to *Mephitis putida* refer to material from Port Kennedy Cave, Pennsylvania, now probably referable to *Osmotherium spelæum*.

The material referred to in the synonymy of *Mephitis mephitis nigra* comes from cave deposits in Pennsylvania.

The material from Frankstown Cave reported on by Peterson (1926, p. 284, fig. 6) has been examined by the writer and is found to present no difference from selected specimens of Recent *M. m. nigra*.

The type specimen of *Mephitis frontata* has been examined and likewise presents no characters of seeming systematic worth to distinguish it from *M. m. mephitica*. As pointed out by Allen (1876, p. 333) the characters relied upon by Coues in distinguishing *frontata* from the living skunk were due to ". . . an abnormal tumidity of the frontal region, arising evidently from disease." (See Plate 5, fig. 5.) Later Howell (1901, p. 16), in commenting on names applied to members of the genus *Mephitis* (*Chincha* of Howell, *op. cit.*), disposed of the name *frontata* with the remark "While the characters assigned to it by him [Coues] are of slight weight, it differs from the living species in dental characters and seems worthy of specific recognition." The present writer, however, fails to find any characters not attributable to the diseased condition of the skull, which would distinguish it from *Mephitis mephitis nigra*.

*Mephitis mephitis elongata* Bangs

- Mephitis elongata*, Simpson (1928, p. 2); Hay (1930, p. 532).

*Remarks*—One lower jaw identified by Simpson (1928, p. 2) as *Mephitis elongata* was found in Pleistocene earth in a cave in the Ocala Limestone (Eocene) one mile northwest of Lecanto, Citrus County, Florida. The form *elongata* is that which occurs in the same region today. The specimen has not been examined by the present writer.



*Mephitis mephitis avia* Bangs

*Mephitis mesomelas avia*, Hay (1930, p. 533).

*Mephitis mephitica*, McGee, (1891, p. 495); Chamberlain (1894, p. 759); Leverett (1899, pp. 42, 124); Hay (1902, p. 766, part); Calvin (1909, p. 342); Baker (1920, pp. 248, 283); Hay (1924, p. 283).

*Mephitis mephitis*, Hay (1914, p. 481).

*Mephitis mesomelas*, Hay (1914, p. 480).

*Mephitis putida*, Trouessart (1904, p. 192, part); Hay (1923, p. 283).

*Mephitis mephitica newtonensis* Brown (1908, p. 175, pl. 16).

*Mephitis mephitis newtonensis*, Hay (1914, p. 32).

*Mephitis mesomelas newtonensis*, Hay (1930, p. 533).

*Mephitis newtonensis*, Hay (1924, p. 252).

Common Skunk, Upham (1895, p. 282).

*Remarks*—The above synonymy applies strictly to allegedly fossil remains. These comprise two finds, from within the range now occupied by *Mephitis mephitis avia* Bangs, of remains not distinguishable from those of the living animal.

The first of these refers to a scapula found in a peat deposit encountered in digging a well at Yarmouth, Des Moines County, Iowa. According to McGee (1891, p. 495) and Leverett (1899, pp. 42, 124) this was identified by True of the United States National Museum as indistinguishable from the common skunk, then known as *Mephitis mephitica*. Obviously the reference of this specimen to *Mephitis mephitis avia* is justified only on grounds of convenience. Since *Osmotherium*, resembling *Mephitis* in parts known, was not yet found when True identified the scapula, there is no guaranty but that the supposed *Mephitis* really belonged to *Osmotherium* or to some other genus. The scapula in question has not been examined by the present writer.

The second find is open to question only on the chance that the remains are those of an animal which in some way entered the Conard Fissure in Newton County, Arkansas, at a time later than the period when most of the remains in the fissure accumulated. The only doubt is that the remains are actually of Pleistocene age. No question exists with reference to the determination of the species as *Mephitis mephitis* and there is good reason, as set forth below, for assigning the material to the subspecies *avia*.

When Brown (1908, p. 175, pl. 16) made skull fragments of *Mephitis*, from the Conard Fissure of Newton County, Arkansas, the basis of the new name *Mephitis mephitica newtonensis*, he compared his materials with the now geographically remote "northern *M. mephitica*" and not, I judge from his account (*op. cit.*), with the race of *Mephitis* which occurs in northern Arkansas today. This I now am able to do by reason of the receipt at the Museum of Vertebrate Zoology of three skulls of *Mephitis mephitis avia* from four and one-half miles southeast of Bergman, Boone County, Arkansas. This locality is approximately sixteen miles northeast of Conard Fissure.

Although Brown (*loc. cit.*) was able to list about twenty-five structural features in which his fissure material differed from the Recent "northern *M. mephitica*," comparisons of the fissure material which Mr. Brown has kindly permitted me to examine, with the three skulls from northern Arkansas, Nos. 51604-06, show that only two of these distinctions apply. These are the greater height of crown of P<sub>4</sub> and the lesser height of the coronoid process. The latter character may be due to wearing away, or chewing away by rodents, of the topmost portion. This part of the process is composed of porous, highly friable, osseous tissue in Recent *Mephitis*, similar, in ontogenetic stage, to the type specimen of *M. m. newtonensis*.



However this may be, each of these two features is exceeded, in each direction, by specimens in a series of thirty-six individuals before me of *Mephitis mephitis occidentalis*. By analogy one would expect an equal range of variation in an equally large series of skulls of the Recent *Mephitis* from northern Arkansas.

It appears therefore desirable to regard the name *Mephitis mephitis newtonensis* as a synonym of the Recent *Mephitis mephitis avia* Bangs.

Measurements indicating the likeness of the fossil and Recent specimens are as given on page 72.

*Mephitis mephitis varians* Gray

*Remarks*—I have examined two skulls of the species *Mephitis mephitis* from Shelter Cave, Dona Ana County, New Mexico. Cranial characters show these to be either *M. m. estor* or *M. m. varians*. Since *M. m. varians* occurs in the region today, these two skulls are referred to that subspecies. The same reference is made of four lower jaws from the same cave. The material mentioned was submitted to the writer by Professor Chester Stock, and is now preserved in the Los Angeles Museum of History, Science and Art.

*Mephitis mephitis holzneri* Mearns

*Mephitis occidentalis*, Wilson (1933, p. 67).

"*Mephitis occidentalis*, the living western skunk; possibly a new species," Osborn (1925, p. 531).

*Mephitis occidentalis* n. subsp., Stock (1925, p. 30).

*Mephitis occidentalis* n. subsp.?, Hay (1927, p. 184).

*Mephitis*, Stock (1930, p. 38).

*Mephitis* sp., Miller, L. H. (1912, p. 78).

*Remarks*—All but one of the citations given above refer to material taken from the asphalt deposits at Rancho La Brea, in southern California. Examination of 17 skulls and 9 lower jaws from this locality, now in the collection of the Los Angeles Museum of History, Science and Art, reveals that they are either *Mephitis mephitis holzneri* or *Mephitis mephitis occidentalis*. Size is the main cranial difference between these two forms; the size of skull gradually decreases from northern California southward to Santa Rosalía, Lower California. Individual variation is great. In view of all this, subspecific identification of a series of skulls alone from one place must be made on the basis of an average as compared with averages from two selected points, one well to the southward near the Lower California-California boundary and one well up in northwestern California. Males are larger than females. By making a tentative determination of sex of these specimens, taking age into account, and tabulating measurements, it is found that the average for adults falls a little nearer that of *holzneri* than to that of *occidentalis*. If by mistake a female was included with the supposed male skulls, or if one or two additional skulls similar to the largest ones were found, the average would be shifted so as to fall nearer that of *occidentalis* than to *holzneri*. The nine lower jaws seem to represent the same race as do the skulls.

Wilson (1933, p. 67) recorded specimens from the Carpinteria asphalt deposit which differed from any Recent ones examined by him in "(1) antero-posterior shortness of M<sub>1</sub> and (2) slenderness of M<sub>1</sub> and P<sub>4</sub>." Of material studied by him I have examined from the collections of the California Institute of Technology four parts of lower jaws bearing the number 138, a fifth lower jaw No. 4 6 BS, 3—4 $\frac{1}{2}$ , and the nearly complete skull No. 1279.

Collection	Catalogue No.	Sex and age	Locality	Width of alveolus of lower canine	Depth of jaw at anterior border of M <sub>1</sub>	Depth of jaw at posterior border of M <sub>1</sub>	Length of M <sub>1</sub>	Length of trigonid of M <sub>1</sub> measured from posterior border of protoconid	Length of trigonid of M <sub>1</sub> measured from notch at posterior base of protoconid	Width of M <sub>1</sub> across metaconid	Width of M <sub>1</sub> across talonid	Length of P <sub>4</sub>	Width of P <sub>4</sub>	Alveolar lengths except at posterior border of P <sub>4</sub>				Length of M <sub>1</sub>	Breadth of M <sub>1</sub>		
														P <sub>3</sub> to anterior border of P <sub>4</sub>	P <sub>3</sub> to anterior border of P <sub>4</sub>	canine to anterior border of P <sub>4</sub>	P <sub>3</sub> to anterior border of P <sub>4</sub>				
A.M.N.H.	.....	yg.	Conard Fissure	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
A.M.N.H.	12428	sad.	Conard Fissure	3.3	6.9	7.5	9.7	5.5	6.2	4.3	4.4	4.3	2.9	9.0	13.0±	7.05	6.3	7.4	.....	.....	.....
M.V.Z.	51604	♂ ad.	16 mi. NE Conard Fissure	3.7	7.9	7.8	9.1	5.3	6.1	4.1	4.3	3.8	2.9	8.0	13.0	6.6	6.5	6.9	.....	.....	.....
M.V.Z.	51605	♂ sad.	"	3.3	7.1	7.9	9.8	5.5	6.5	3.8	3.9	4.1	2.8	8.4	13.1	7.0	6.5	7.1	.....	.....	.....
M.V.Z.	51606	♂ sad.	"	3.7	7.7	7.3	10.3	5.9	6.8	4.3	4.8	4.5	2.9	9.0	13.5	6.9	6.6	7.9	.....	.....	.....

I am unable to distinguish the lower jaws from selected ones of either *M. m. holzneri* or *M. m. occidentalis*. The right M<sub>1</sub> of the skull measures 7.3 mm. anteroposteriorly along the outside border and 8.2 mm. transversely. Of Recent specimens examined, No. 4978, M.V.Z., *M. m. occidentalis* from Stockton, California, has the corresponding measurements exactly the same, and *M. m. holzneri*, No. 2249, M.V.Z., from 6000 feet elevation, Strawberry Valley, in the San Jacinto Mountains, measures 7.0 mm. anteroposteriorly and 7.85 mm. transversely. Though the tooth of No. 2249 is smaller than that of the fossil, the proportion of breadth to length is almost the same. P<sub>4</sub> of the fossil skull measures 8.0 mm. anteroposteriorly and 5.8 mm. transversely, as opposed to corresponding measurements of 8.1 and 5.8 in a Recent skull, No. 54952, M.V.Z., of *M. m. occidentalis* from Berkeley, California. Other skulls of *occidentalis*, and those of *holzneri* too, show fourth upper premolars both relatively broader and relatively narrower than P<sub>4</sub> of the fossil. Thus it may be said that the features thought by Wilson (*loc. cit.*) to distinguish the fossil specimen can be duplicated in selected Recent specimens of *holzneri* and *occidentalis*. The size of the fossil skull is nearer the average for *occidentalis* than it is to that of *holzneri*. However, Wilson (*loc. cit.*) remarks that his second skull, not examined by me, was smaller. In any event, a greater number of skulls from this asphalt deposit would be required to permit of one making a satisfactory subspecific determination of the remains found there. The material is mentioned here under the name *M. m. holzneri* because the range of that subspecies was stated by the last reviser (Howell, 1901) to include the region of Carpinteria.

On October 20, 1932, I found, among material being prepared for study at the California Museum of Palæontology, and not at the time given catalogue numbers, the lower jaw bearing M<sub>1</sub> and P<sub>4</sub> of a young *Mephitis mephitis* taken from the asphalt deposits at McKittrick in Kern County, California. The specimen is not identifiable as to subspecies and is here referred to *holzneri* on geographic grounds.

#### *Mephitis mephitis occidentalis* Baird

*Mephitis occidentalis*, Sinclair (1903, p. 711; 1904, p. 16); Furlong (1904, p. 55; 1906, p. 245); Miller, L. H. (1912, pp. 70, 73); Stock (1918, pp. 468-469; 1925, p. 113); Merriam and Stock (1925, p. 10); Hay (1927, pp. 214, 215, 223; 1930, p. 533).

*Remarks*—The citations given above refer to material obtained from Potter Creek Cave, Samwel Cave, and Hawver Cave, in northern California. The specimens are preserved in the University of California Museum of Palæontology, where they have been examined by the writer. No features are revealed by which the specimens from the caves can be distinguished from ones of the living *Mephitis mephitis occidentalis*.

#### Genus CONEPATUS Gray

Gray, Charlesworth's Mag. Nat. Hist., vol. 1, p. 581. November, 1837.

*Diagnosis*—Skull similar in size to that of *Mephitis*; flattened in frontal region and deepest in temporal region; mastoid bullæ slightly inflated; posterior margin of palate behind posterior borders of last upper molars; anteroposterior and transverse diameters of M<sub>1</sub> each more than outside length of P<sub>4</sub>; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{2}{3} \frac{1}{2}$ ; infraorbital canal opening above point of contact of M<sub>1</sub> and P<sub>4</sub>; metaconule of M<sub>1</sub> not distinct; inferior



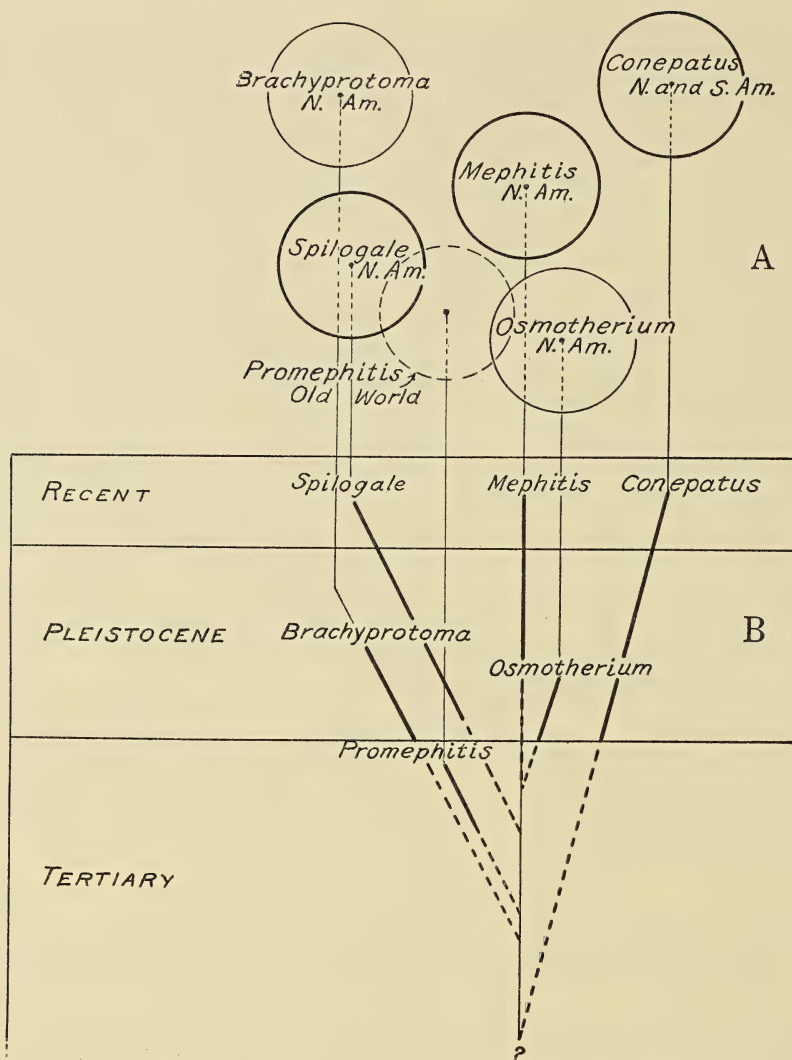


FIG. 4—Two diagrams showing hypothetical relationships of six genera of the Mephitinae. A, view looking back into time; B, side view of phylogenetic tree.

margin of mandible bent; angle of mandible represented by flattened face in horizontal plane eliminating the step seen in *Mephitis*; coronoid process low and inclined posteriorly; in MI trigonid shorter than talonid, metaconid high and distinct from protoconid, hypoconid low, entoconid high and separated from protoconid by a distinct notch.

*Genotype*—*Conepatus humboldtii* Gray.

*Remarks*—So far as known, no members of the genus have been found in North America in deposits thought by writers to be earlier than the Recent. The genus is included here to complete the list of genera of the true skunks and to permit a comparison of the generic characters (see diagnosis) with those of the four other genera of the subfamily Mephitinae that have been found in North American deposits older than Recent.

## Genus LUTRA Brisson

Brisson, Regn. Anim., ed. 2, p. 201.

*Diagnosis*—Skull ranging in basilar length from 50 to 135 mm.; flattened in longitudinal dorsal outline; tympanic bullæ flattened and not in contact with paroccipital processes; palate behind upper molars; diameter of infraorbital canal greater than that of alveolus of canine; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{4}{3} \frac{1}{2}$ ; M1 rhombic and large; P4 with basined deutercone; in M1 talonid and trigonid of roughly equal length, metaconid large, talonid basined.

*Genotype*—*Lutra* Brisson = *Mustela lutra* Linnæus.

*Remarks*—In North America, north of Mexico, all the living species and subspecies of river otter, with seeming correctness, are referred (see Pohle, 1920, p. 221) to the single species *Lutra canadensis* (Schreber) which is one species of the *platensis* group of the subgenus *Lutra*.

*Lutra canadensis* cf. *lataxina* (F. Cuvier)

*Lutra canadensis*, Allen (1876, p. 333); Hay (1902, p. 769).

*Lutra canadensis lataxina*, Pohle (1920, p. 87).

*Lutra parviuspis* Gidley and Gazin (1933, pp. 349-351, fig. 3).

*Lutra rhoadsi*, Schlosser (1899, p. 362; 1902, p. 142); Baker (1920, p. 208); Pohle (1920, pp. 87-89).

*Lutra rhoadsii* Cope (1896, pp. 391-392); Trouessart (1898, p. 285); Cope (1899, pp. 238-239, pl. 18, figs. 11, 11a); Hay (1902, p. 769); Rhoads (1903, p. 231); Baker (1920, pp. 215, 397); Hay (1923, p. 312; 1930, p. 538).

*Remarks*—Allen (1876, p. 333) recorded *Lutra canadensis* from caves in Pennsylvania and found the remains to be indistinguishable from those of the Recent otter living in the same region. The present writer has not examined this material and can only add that the subspecies of otter occurring in the lower parts of Pennsylvania now is recognized under the name *L. c. lataxina*.

I have examined the now available material on which Cope based the name *Lutra rhoadsii*. This is a right lower jaw and a crushed mass of bone showing fractured dentary material at one point. The latter may, or may not, have constituted the basis for his remarks (1899, p. 239) about a "superior tubercular." I have not seen the fragment of a left lower jaw figured (*op. cit.*, pl. 18, fig. 11a) by Cope.

This examination leads me to believe that Pohle (1920, p. 87) was correct in placing *Lutra rhoadsii* as a synonym of *Lutra canadensis lataxina*. At any rate the material on which the name *rhoadsii* was based presents no characters that distinguish it from *L. c. lataxina*, the race which occurs in the same region today.

The right lower jaw has two major lines of fracture; one is at the anterior root of M1 and the other extends vertically through the coronoid process. These are shown in Cope's figure (*op. cit.*, pl. 18, fig. 11). In addition there are other, smaller, lines of fracture not shown in the illustration. These fractures have permitted pressure of the matrix to alter the original shape of the jaw. The relatively straight inferior margin of the jaw remarked on by Cope (*loc. cit.*) and also the present shape of the coronoid process, as well as its position relative to the horizontal ramus, seemingly are to be explained by this post-mortem alteration of shape. Each of the other allegedly distinctive features of *rhoadsii*, even to the transverse position of the premolar, next, adjacent, to the canine, on which Cope placed great systematic weight, is covered by individual variation in three skulls of



*Lutra* from Louisiana. The right lower jaw from the Port Kennedy bone deposit permits the following measurements: Posterior border of M<sub>2</sub> to anterior alveolar border of P<sub>3</sub>, 30.9; alveolar length of P<sub>3</sub> and P<sub>4</sub>, 13.0; angle of mandible to anterior alveolar border of P<sub>3</sub>, 54.3; depth of ramus at posterior border of P<sub>4</sub>, 11.5.

The name *Lutra parviuspis* Gidley and Gazin was based on a preorbital part of a skull lacking the incisors, canines and first upper premolars, but supplemented by the posterior part of the skull in which the larger part of the basiscranial region is well preserved. This specimen from the Cumberland Cave deposit, Maryland, was regarded by the describers as intermediate between the larger-toothed South American otters and the smaller-toothed forms of North America.

Selecting at random 28 river otter skulls in the Museum of Vertebrate Zoology—a lot comprising 25 skulls from the Pacific Coast (Alaska to California) and 3 from the coast of western Louisiana—direct comparison of the fossil shows that every character mentioned by the original describers as diagnostic of *Lutra parviuspis* is duplicated in one or another of the Recent specimens. More in detail: Every linear measurement given for the fossil is exceeded in each direction; main outer cusps on the cheek teeth are found which are as low, narrow, and as lateral in position as in the fossil; the diameter of the canine is less in the fossil than in selected Recent individuals; one skull from southeastern Alaska and each of the three from Louisiana has on P<sub>2</sub> and P<sub>3</sub> the posterointernal basin which occurs in the fossil; variations in size and shape of P<sub>4</sub> exist which correspond with the condition found in the fossil. The anteroposterior shortness of M<sub>1</sub> in comparison with the outside length of P<sub>4</sub> is another feature thought by the original describers to differentiate the fossil from living North American otters. The measurements, length of P<sub>4</sub>, 12.7 mm., and length of outer moiety of M<sub>1</sub>, 8.3, show that M<sub>1</sub> is 65.3 per cent as long as P<sub>4</sub>. In one Recent specimen, No. 21246, from southeastern Alaska, the measurements are 13.6 and 8.8, giving a percentage of only 64.6, which is less than in the fossil. The remaining Recent specimens have corresponding percentages ranging from 68 to 81, and thus greater than in the fossil.

In comparison with a specimen of *Lutra provocax* from the Rio Chubut, Chubut, Argentina, the fossil has relatively smaller upper carnassials and molars essentially as occur in North American forms. Though I have been able to find each of the features at one time regarded as diagnostic for the fossil duplicated in the Recent specimens, it is true that no one of the 28 Recent specimens presents exactly the same combination of characters as the fossil. However, if any one of the 28 Recent specimens is selected, none of the remaining 27 presents exactly the same combination of characters, either. My comparison brings out, however, that anyone of the three Louisiana-taken specimens combines more of the features found in the fossil than does any Recent specimen from the Pacific Coast. These specimens from Louisiana, among named races of *Lutra canadensis*, seemingly are nearest *Lutra canadensis lataxina*, the geographic race of living otter occurring also in the vicinity of Cumberland Cave. That Recent specimens of *Lutra canadensis* from Maryland and near-by regions are not available in series, for comparative purposes, is regretted and this lack leaves some uncertainty as to the consubspecificity of the fossil animal and the one living there today.

Summed up, study of the fossil specimen serving as basis for the name *Lutra parviuspis* fails to reveal any structural features by which it can be distinguished from selected specimens of the full species *Lutra canadensis*



and, on the evidence available, the name *Lutra parviuspis* seems best placed in the synonymy of *Lutra canadensis lataxina*.

When the above account was in press, Goldman's (Proc. Biol. Soc. Washington, vol. 48, pp. 178-186. November 15, 1935) paper characterizing 10 additional kinds of North American otters was received. Some of the names newly proposed by him apply to Recent specimens used in identifying the fossil remains from the eastern United States. For example the above-mentioned Louisiana-taken specimens probably belong to the race *L. c. texensis*. Thus, although the two fossil otters be of the species *canadensis*, the subspecific identity of the fossil animal in the eastern United States must remain an open question until series of Recent specimens from there are employed in comparisons.

*Lutra canadensis* cf. *vaga* Bangs

*Lutra canadensis*, Sellards (1916, p. 152; 1917, pp. 16-17); Hay (1923, p. 382; 1927, p. 274); Hay (1930, p. 537, part).  
"Otter," Cooke (1926, p. 445).

*Remarks*—The literature cited above refers to remains from Vero and Melbourne, Florida. The subspecies of otter found there at the present time is *L. c. vaga* and the remains, which have not been seen by the present writer, are tentatively referred to that form as an aid in nomenclatural reference.

*Lutra* cf. *canadensis interior* Swenk

*Lutra*, Matthew (1918, p. 228); Hay (1924, p. 304).

*Remarks*—In 1918 (p. 228) Matthew recorded fragmentary remains identified as "*Lutra*" from beds, underlying the sandhill deposits, along the Middle Loup Fork River west of Seneca, Nebraska, judged to be of Pleistocene age. Hay (1924, p. 304) merely refers to Matthew's (*loc. cit.*) mention of the remains. The Recent otter of the region is *L. c. interior* Swenk and the fossil remains are tentatively assigned to this form as an aid in nomenclatural reference.

*Lutra canadensis* cf. *pacifica* Rhoads

*Lutra canadensis*, Matthew (1902, p. 320); Miller, L. H. (1912, p. 81); Stock (1925, p. 195); Hay (1927, pp. 191, 243); Hay (1930, p. 537, part).

*Remarks*—In the literature mentioned above there are recorded remains of *Lutra canadensis* from Silver Lake, Lake County, Oregon, and Fossil Lake, Oregon. None of the remains has been examined by the present writer and a tentative reference to *L. c. pacifica*, the subspecies which occurs in that region today, is made on the basis of readier nomenclatural reference.

Genus TAXIDEA Waterhouse

Waterhouse, Proc. Zool. Soc. London, 1838, p. 153.

*Diagnosis*—Skull ranging in basilar length from 100 to 130 mm.; occiput depressed; facial angle steep; tympanic bullæ highly inflated but not in contact with paroccipital processes; palate behind upper molars; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{1}{2}$ ; M1 triangular, often with cusps arranged in rows, which rows, when present, are transverse (to long axis of skull); P4 with accessory cusp behind deuterocone; in M1 trigonid longer than talonid, metaconid large, hypoconid and entoconid large; talonid often with one, two or three additional cusps.

*Genotype*—*Meles labradorius* Gmelin = *Ursus taxus* Schreber.

*Remarks*—Living members of the genus *Taxidea* have in late years been referred to a single species. Examination of specimens in several of the larger mammal collections of North America leads the writer to subscribe to this arrangement. Also, this examination has revealed an amount of geographic variation which, as I see it, justifies the recognition of only four subspecies (geographic races). These are as follows:

*Taxidea taxus taxus* (Schreber).

- 1778. *Ursus taxus* Schreber, Säugethiere, vol. 3, p. 520. 1778.
- 1784. *Meles taxus* var. *americanus* Boddaert, Elenchus animalium, vol. 1, p. 136. 1784.
- 1788. *Ursus labradorius* Gmelin, Systema Naturæ, 13 ed., T. 1, p. 102. 1788.
- 1825. *Meles jeffersonii* Harlan, Fauna americana, p. 309. 1825.
- 1878. *Taxidea sulcata* Cope, Proc. Amer. Philos. Soc., vol. 17, p. 227. 1878.
- 1894. *Taxidea taxus*, Rhoads, Amer. Nat., vol. 28, p. 524. June, 1894.
- 1918. *Taxidea taxus phippisi* Figgins, Proc. Colo. Mus. Nat. Hist., vol. 2, No. 2, p. 1. April, 1918.
- 1933. *Taxidea marylandica* Gidley and Gazin, Jour. Mammalogy, vol. 14, p. 352. November 13, 1933.

*Type Locality*—Labrador and Hudson Bay (probably southwest of Hudson Bay).

*Range*—Southwestern Ontario, Michigan, Wisconsin, northern Indiana, northern Illinois, northern Iowa; northwest to central Alberta; southward to northern New Mexico, and northern Arizona; westward over the Sierra Nevada and in the Great Basin northward into southern British Columbia.

*Taxidea taxus neglecta* Mearns.

- 1891. *Taxidea americana neglecta* Mearns, Bull. Amer. Mus. Nat. Hist., vol. 3, p. 250. June 5, 1891.
- 1901. *Taxidea taxus neglecta*, Miller and Rehn, Proc. Boston Soc. Nat. Hist., vol. 30, p. 218. December 27, 1901.

*Type Locality*—Fort Crook, Shasta County, California.

*Range*—Northern California thence southward west of the Sierra Nevada to the Tehachapis, thence along the coast and in the Coast Range to at least 31°30' north latitude, Lower California, Mexico.

*Taxidea taxus berlandieri* Baird.

- 1857. *Taxidea berlandieri* Baird, Mamm. N. Amer., p. 205. 1857.
- 1865. *Taxidea americana* Var. *Californica* Gray, Proc. Zool. Soc. London, 1865, p. 141. 1865.
- 1895. *Taxidea taxus berlandieri*, Allen, Bull. Amer. Mus. Nat. Hist., vol. 7, p. 256. June 29, 1895.

*Type Locality*—Llano Estacado, Texas, near boundary of New Mexico.

*Range*—Texas, New Mexico and Arizona below Boreal zones, southern Nevada, Mojave and Colorado deserts of California, and for an undetermined distance into Mexico.

*Taxidea taxus infusca* Thomas.

- 1891. *Taxidea americana infusca* Thomas, Proc. Zool. Soc. London, 1897, p. 899. April 1, 1898.

*Type Locality*—Santa Anita, Lower California, Mexico.

*Range*—Peninsula of Lower California, Mexico. Northward extent of range on Peninsula not determined.



The distinguishing characters, of these four subspecies, as known to the writer, may be summarized as follows:

- A. Size averaging larger; mid-dorsal white stripe generally not extended posteriorly beyond shoulders.
  - 1. Coloration grayish ..... *taxus*
  - 2. Coloration reddish ..... *neglecta*
- B. Size averaging smaller; mid-dorsal white stripe generally extended posteriorly beyond shoulders.
  - 1. Coloration grayish (mid-dorsal white stripe not markedly wider at nape than elsewhere ?) ..... *berlandieri*
  - 2. Coloration reddish; mid-dorsal white stripe markedly wider at nape than elsewhere ..... *infusca*

It may be remarked that an examination of more than 200 skins and approximately 300 skulls has failed to reveal any characters other than those mentioned above that are judged to be of taxonomic worth. Also, the ones mentioned above are only average characters—they apply when a number of specimens are compared but do not always serve to distinguish individual specimens. The skull differences, so far as I have been able to see, are ones of average size. Naturally, therefore, the allocation of isolated Pleistocene specimens to a given subspecies is not to be accomplished with any great degree of certainty.

#### *Taxidea taxus* cf. *taxus* (Schreber)

- Taxidea taxus*, Hay (1902, p. 765); Rhoads (1903, p. 231); Baker (1920, pp. 214, 397); Hay (1923, p. 312; 1924, p. 270; 1927, p. 251; 1930, p. 535).  
*Taxidea* cf. *taxus*, Cook (1931, pp. 273–275).  
*Taxidea americana*, Cope (1889, p. 162; 1899, p. 239); Schlosser (1902, p. 142); Frech and Geinitz (1904, p. 36); Baker (1920, p. 208).  
*Taxidea marylandica* Gidley and Gazin (1933, pp. 352–354, figs. 5, 6).  
*Taxidea sulcata* Cope (1878, p. 227; 1889, p. 162); Dall and Harris (1892, p. 228); Trouessart (1898, p. 252); Hay (1902, p. 765).  
*Taxidea sulcata* (= *americana*), Matthew (1902, p. 321); Stock (1925, p. 199).  
*Taxidea* sp. indet., Hay (1923, p. 350).  
 “Badger”, Gidley (1920, p. 282).

*Remarks*—Remains referred to in the above synonymy have been recorded from the Port Kennedy bone deposit, Pennsylvania; the Cumberland Cave deposit, Maryland; from Logan County, Kansas; from two miles northeast of Spring Ranch, on Pawnee Creek, about twenty-five miles northeast of Hastings, Nebraska; from the “Oregon Desert” (Cope, 1889, p. 162); and from Franklin County and the “Equus beds” (Hay, 1902, p. 765) of the state of Washington.

Except the two localities first mentioned, all the finds are within the present range of the living *Taxidea taxus taxus*. No badgers in historic time are known from so far east in North America as Pennsylvania and Maryland.

None of the remains has been regarded by writers as representing a species or subspecies distinct from the living species except those from Fossil Lake, Oregon, described by Cope (1878, p. 227) as *Taxidea sulcata*, new species, and those from the Cumberland Cave deposit, Maryland, named by Gidley and Gazin (1933, p. 352) as *Taxidea marylandica* new species. The assumedly distinctive characters of *T. sulcata*, namely the “abbreviation of the anterior portion of the dental series,” seemingly with reference to the upper jaw, and the arrangement of the cusps of M<sub>1</sub> in two transverse rows, later (1889, p. 162) were recognized by Cope as not of taxonomic worth. Accordingly he (*loc. cit.*) relegated *Taxidea sulcata* Cope to the synonymy of *Taxidea americana* [= *Taxidea taxus* (Schreber)]. At the American



Museum of Natural History in New York the writer was privileged to examine the type specimen (now bearing catalogue No. 8649, Am. Mus. Nat. Hist.) and found no characters which distinguish the remains from selected specimens of the Recent *Taxidea taxus taxus* from Nevada used for comparison.

Sole basis for here stating that the type specimen of *Taxidea sulcata* Cope came from Fossil Lake, Oregon, is furnished by the data with the type specimen in the American Museum. A definite locality was not given in the original description.

In addition to the left upper dentition and maxillary bone designated by Cope (1878, p. 227) as the type specimen, there are in the American Museum two lower jaws bearing the same catalogue number and accompanied by data identical with that ascribed to the upper jaw. These two mandibular rami represent right and left sides and in so far as can be judged by degree of wear on the teeth might well have belonged to the individual represented by the left upper maxilla.

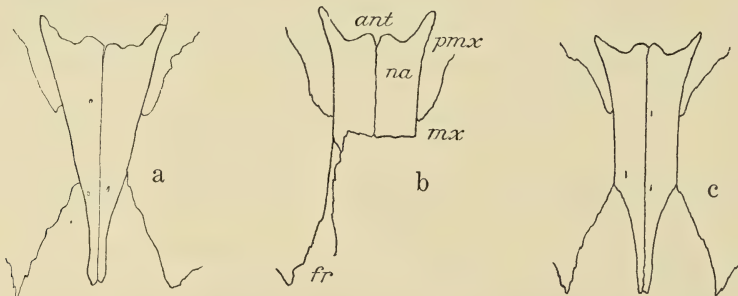


FIG. 5—Dorsal view of nasal bones of three specimens of *Taxidea taxus taxus* (Schreber) to show variation in shape. ant., anterior end of nasals; fr., frontal; mx., maxilla; na., nasal; pmx., premaxilla.

a. No. 24756, Mus. Vert. Zool., ♂; Recent; Mountain City, Elko County, Nevada.

b. No. 7990, U. S. Nat. Mus., probably ♂; Pleistocene; Cumberland Cave, Maryland. Type specimen of *Taxidea marylandica* Gidley and Gazin.

c. No. 44731, Mus. Vert. Zool.; sex ?; Recent; Pahrnagat Valley, Lincoln County, Nevada.

Study of *Taxidea marylandica* fails to reveal any morphological features distinguishing it from specimens of the living badger, *Taxidea taxus taxus*. The type specimen of *T. marylandica* consists of the skull and lower jaws, a series of vertebræ and the proximal half of the right humerus. The specimen, U. S. Nat. Mus., No. 7990, is a young individual, from Cumberland Cave of Pleistocene age, obtained by J. W. Gidley, four miles northwest of Cumberland, Maryland. So far as the present writer knows no other specimens of *Taxidea* were recovered from the deposit.

Morphological features mentioned by the original describers as diagnostic or otherwise characteristic of *Taxidea marylandica* were looked for individually and, with two exceptions, were found to be duplicated in one or more of the 125 Recent specimens used for comparison. One exception has to do with the occiput which the describers rightly characterize as depressed when seen in lateral view. Some of the Recent specimens have the dorsal outline of the skull over the occipital region more nearly straight and others have it more sloping than in the fossil specimen though none exhibits the

exact contour of the latter. Since the condition in question is, in a sense, exceeded in both directions among Recent specimens, it is regarded as being of but slight if any taxonomic worth.

The second exception has to do with the nasals which the describers thought were as wide at the anterior ends of the frontals as at the posterior ends of the premaxillæ. In every Recent specimen examined by them, and in all those studied by me, the width across the nasals was less at the anterior end of the frontals than at the ends of the premaxillæ. After studying the type of *T. marylandica* I am confident that it, too, had the nasals narrower posteriorly and thus does not differ in this respect from certain Recent specimens. In this connection it must be pointed out that the posterior part of the nasals and adjoining right frontal bone are severely fractured and in part missing. It is only on the left side that the anterior end of the frontal bone is preserved. Actually the width of the nasals at this point can not be measured; it has to be estimated. It is true that the outer side of the left nasal is almost parallel for a short distance in this region (see fig. 5, b) with the mid-dorsal line, but it is not quite parallel. Judging from the one margin preserved, the two margins are thought to have borne essentially the same relative positions as those shown in figure 5, c. This shape is different from that (see fig. 5, a) most often found in Recent *Taxidea*, but not different from that found in several Recent specimens, one of which is represented in figure 5, c. The following measurements of three Nevada-taken Recent specimens indicate a wide variation in shape of nasals and the measurements of No. 47205, though actually smaller than in the fossil bear about the same proportional relation to one another.

	M.V.Z. No.	M.V.Z. No.	M.V.Z. No.
	44731	47205	45904
Width of nasals at posterior ends of premaxillæ.....	8.6	8.9	11.5
Width of nasals at anterior ends of frontals.....	8.3	8.6	9.6

The type specimen of *Taxidea marylandica*, then, is not found to differ from Recent specimens of *Taxidea taxus taxus* in shape of nasals or in other described features. It may be added that search for diagnostic features additional to ones mentioned in the original description has been in vain. Considering the age and geographic origin of the Cumberland Cave specimen, one would expect it to belong to a species or subspecies different from the Recent kinds. However, no characters have been found to show that it is different. Accordingly, *Taxidea marylandica* Gidley and Gazin is placed in the synonymy of *Taxidea taxus taxus* (Schreber).

Of materials from Pleistocene deposits here referred to *Taxidea taxus* cf. *taxus* I have examined only the skull and lower jaws (not the series of vertebrae and portion of humerus, of the type specimen of *Taxidea marylandica* and the materials which gave basis for the name *Taxidea sulcata* Cope.

#### *Taxidea taxus* cf. *neglecta* Mearns

- "*Taxidea* n. sp.", Miller, L. H. (1912, pp. 70, 73); Merriam and Stock (1925, p. 10); Hay (1927, p. 215).  
 "*Taxidea* n. sp. (?)", Sinclair (1904, p. 17); Stock (1918, p. 468; 1925, p. 113).  
 "*Taxidea*, possibly n. sp.", Stock (1925, p. 30); Osborn (1925, p. 531).  
*Taxidea* species, Wilson (1933, p. 67).  
 "*Taxidea* (?) sp. nov.", Sinclair (1903, p. 711).  
 "*Taxidea* sp. indet. or nov.", Hay (1927, p. 184).  
 "badger (*Taxidea*)", Stock (1930, p. 38).  
 "*Taxidea*", Anonymous (1871, p. 139).



*Remarks*—The mention in literature of badgers of the genus *Taxidea*, indicated above, refers to materials from four Pleistocene deposits. These are the Rancho La Brea asphalt deposits in California near Los Angeles, the Potter Creek and Samwel Cave deposits in Shasta County, and the Carpinteria asphalt deposits in Santa Barbara County. During the past ten years the writer has taken opportunity to compare carefully the fossil remains from each of the three first-mentioned localities with Recent specimens from California. In each instance no structural features in the fossil remains could be found which gave basis for designating the kind of animal they represented as different from Recent *Taxidea taxus neglecta* found in the same regions today.

Without information as to the actual size of the calcaneum from Carpinteria which Wilson (1933, p. 67) found "approximates in size the comparable element in *Taxidea taxus berlandieri*," it is impossible to judge of its subspecific relation. However, I would be surprised if the size were less than in the smallest individuals of *T. t. neglecta*, the race which is thought to occur in the deposits of Rancho La Brea and McKittrick.

In addition to these remains, the writer has examined specimens from the McKittrick asphalt deposits, which at the present writing are being prepared for study and are not yet provided with catalogue numbers. This material, in the University of California Museum of Palæontology comprises three skulls, six lower jaws and the larger part of the body skeleton of one individual. In the collection of vertebrate fossils at the California Institute of Technology, from locality 138, there are available parts of three skulls and four lower jaws. Comparisons fail to reveal any structural features distinguishing the fossil specimens from ones of the Recent animal found in Kern County.

*Taxidea taxus* cf. *berlandieri* Baird

Plate 5, figs. 3, 3a, 4, 4a

*Taxidea robusta* Hay (1921, pp. 631-632, pl. 119, figs. 3-5; 1923, p. 9; 1930, p. 535).

*Remarks*—*Taxidea robusta* Hay (1921, p. 631) was based on a left ulna, No. 10208, U. S. Nat. Mus., lacking the styloid process and part above the greater sigmoid cavity, and a second piece consisting of the right pubic bar and a part of the ischium of the right side of the pelvis. These two pieces, of which the ulna is designated as the type specimen, are said by Hay (1921, p. 617) to have been taken "... at the Val Verde Copper Mines, at Anita, a station on the Grand Canyon branch of the Santa Fe Railroad, 40 miles north of Williams and 20 miles south of the Grand Canyon."

The characters indicated by Hay as distinguishing his fossil species from the Recent species were, in the ulna, greater stoutness, ridge on inner face extending from the coronoid process to the distal end rather than absent in middle third; groove, on outer side, extending from sigmoid cavity only halfway to distal end instead of nearly to distal end, and in the innominate bone, narrow rather than broad, and thick rather than thin.

On comparing these two fossil bones with corresponding elements of 9 specimens of *Taxidea taxus* of similar ontogenetic stage from Nevada and California, it is seen that No. 11331, ♂, Mus. Vert. Zool., has an ulna which agrees almost precisely with that of the fossil. Of the other Recent specimens, some are stouter and some are weaker; some have the ridge and groove mentioned by Hay, better developed and longer and some have this shorter and less well developed. In the innominate bone, greater thickness and



lesser thickness than in the fossil is to be seen among Recent specimens. The same is true of the narrowness.

In short, the morphological features noted by Hay as diagnostic of his fossil species, *Taxidea robusta*, and additional features noted by me as possibly of the same nature, in every instance fall within the range of individual variation noted in a series of nine Recent specimens. Although the fossils may belong to an animal that is systematically separable from any Recent badger, no characters to indicate this are apparent. Accordingly *Taxidea robusta* Hay is placed in the synonymy of the Recent badger. Since the geographic point of origin of the fossil badger falls within the range ascribed to the Recent subspecies *T. t. berlandieri* the name *Taxidea robusta* Hay seemingly is best placed as a synonym of *Taxidea taxus berlandieri* Baird.

#### Genus GULO Pallas

Pallas, Spicil. Zool., fasc. 14, p. 25.

*Diagnosis*—Skull ranging in basilar length from 110 to 140 mm., facial angle steep; tympanic bullæ moderately inflated and separate from paroccipital processes; palate behind upper molars; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{4}{4} \frac{1}{2}$ ; inner moiety of M<sub>1</sub> larger than outer; P<sub>4</sub> with simple deuterocone; in M<sub>1</sub> talonid longer than trigonid, metaconid absent, talonid barely semitrenchant and with single median, longitudinal ridge.

*Genotype*—*Gulo sibiricus* Pallas = *Ursus gulo* Linnæus.

*Remarks*—This living genus, of circumpolar distribution in the Boreal life zones, is known in the Pleistocene of North America from two deposits as described under the account of the species.

#### *Gulo gidleyi* new species

*Gulo luscus*, Cope (1899, pp. 229-230); Schlosser (1902, p. 141); Hay (1902, p. 768); Rhoads (1903, p. 229); Baker (1920, p. 397); Hay (1923, pp. 312, 316, 350; 1930, p. 531).

*Gulo* cf. *luscus*, Gidley and Gazin (1933, p. 344).

"Wolverine", Gidley (1920, p. 282).

*Type*—Cranium, lacking the right zygomatic arch, canines and incisors, probably male, No. 8176, U. S. Nat. Mus., Division of Palæontology; Cumberland Cave, 4 miles northwest of Cumberland (Gidley and Gazin, 1933, p. 343), Maryland; Pleistocene age; collected by J. W. Gidley in 1914.

*Referred specimens*—In the Academy of Natural Sciences of Philadelphia, from the Port Kennedy bone deposit, right bank of Schuylkill River, two miles below Valley Forge, Upper Merion Township, Montgomery County, Pennsylvania, three left lower jaws, one fragment of a right lower jaw and one left P<sub>4</sub>, each bearing the catalogue number 63. In the U. S. National Museum, from the type locality, in addition to the type, No. 8194, left maxilla lacking incisors and P<sub>3</sub>; No. 8215, complete upper dentition and skull anterior to the plane of the last upper molars; Nos. 12347 and 12351, left lower jaws; Nos. 12348, 12349 and 12350, right lower jaws.

*Diagnosis*—A species of the genus *Gulo* distinguished from the North American Recent wolverines by about 8 per cent smaller size in linear dimensions of teeth, and by short, broad upper third premolar, the crown width of which amounts to more than 63 per cent of the crown length.

*Remarks*—Gidley (1920, p. 282) and Gidley and Gazin (1933, p. 344) reported the wolverine as found in the Cumberland Cave deposit and Hay

(1923, p. 350) refers to this statement by Gidley. Otherwise the citations to literature given above all pertain to the remains found in the Port Kennedy bone deposit.

Among twenty-seven Recent skulls of *Gulo* (9 from Alaska, 8 from British Columbia, 5 from California; and in the United States National Museum, No. 110281, ♂, Minnesota; No. 67370, ♀, Montana; No. 137051, ♀, Lake St. Croix, Mackenzie; No. 80291, ♀, mouth Stuart River, Yukon; No. 188244, ♂, Godbout, Quebec) none has the length of P<sub>4</sub>, the breadth of M<sub>1</sub> taken through the base of the anterior cusp, or the distance from the posterior border of M<sub>1</sub> to the anterior border of P<sub>4</sub>, so small as are the corresponding measurements in the largest of the three lower jaws from the Port Kennedy bone deposit. Also, in only two of the Recent specimens, both females (see measurements) is M<sub>1</sub> as short and in only one of these two females is P<sub>4</sub> as short as in the fossils. However, if the breadths of the teeth be divided by the lengths, the resulting expression of proportions in the fossils is seen to be exceeded in both directions in the series of Recent specimens. Thus, there remains as distinctive of the lower teeth of the Port Kennedy animal only smaller size.

Five additional lower jaws (see measurements) from Cumberland Cave also have teeth averaging much smaller than in Recent specimens. These five provide some measurements which exceed the minimum measurements for Recent animals, but the minima and maxima of the Cumberland Cave material also falls well below the corresponding limits for Recent specimens. There are available also from Cumberland Cave three specimens which provide the upper dentition. Though these fossil specimens are small in all parts measured, the smallest of the Recent females is of lesser size except the length of P<sub>3</sub> which is less in the fossils. Another peculiarity of P<sub>3</sub> in the fossils is its greater breadth relative to its length. The breadth is 65 and 66 per cent of the length. In 22 Recent specimens examined in this regard, the breadth averages 58 (54 to 61) per cent of the length with one exception. The exception, No. 43631, from the Bowron Lake region of British Columbia, has the breadth of P<sub>3</sub> amounting to 64.5 per cent of the length. However, the tooth in No. 43631 has an enlarged cingulum posteriorly only and is not of the generally broad character throughout found in the fossils.

On the face of it, one might conclude that the wolverine of the Port Kennedy bone deposit and Cumberland Cave averages smaller than the North American Recent wolverine, but overlaps somewhat in size, and let the matter rest there. However, other facts are to be taken into account. One is that wolverines show a secondary sexual difference in size, as do most mustelids. So far as I can ascertain no proportional differences certainly permit one to identify the sex of a given skull of a wolverine. The males are larger, the females smaller. How much difference exists in size, even Recent specimens available do not tell us, for only a few of them are sexed. Of course, the limited fossil material does not permit of segregation according to sex. Judging from the difference in size displayed by a few males and females of which the sex is certainly known, the average difference in size between the two sexes of *Gulo luscus* is about two-thirds as much as in *Martes pennanti*.

The probabilities are, then, that the largest of the eleven fossil specimens are males and the smallest are females. In Recent specimens we know that the smallest specimens are females and that several of the largest are males. Also, it is probable that if the sex of each specimen, fossil and Recent, were



known, the largest of the fossil males would be smaller than the smallest Recent male and that the largest fossil females would be smaller than the smallest Recent female. This probability is so great that, when considered in conjunction with the difference in shape of  $P_3$ , designation of the Pleistocene populations as a kind distinct from the living animal seems in order.

*Measurements of teeth of Gulo*

Locality	Geologic age	Catalogue No.	Collection	Length of $M_1^1$	Breadth of $M_1^1$	Length of $P_4^1$	Breadth of $P_4^1$	Inclusive length $M_1^1$ to $P_4^1$
Port Kennedy	Pleistocene	63	Phila.	18.7	7.9	10.2	5.5	28.1
" "	"	63	"	20.0	7.9	10.0	5.9	29.5
" "	"	63	"	.....	8.0	10.6	5.9	28.5±
Cumberland Cave	"	12347	U.S.N.M.	19.6	8.2	10.3	6.0	29.1
" "	"	12348	"	19.7	8.6	10.7	6.3	29.4
" "	"	12349	"	.....	.....	10.3	6.0	.....
" "	"	12350	"	21.1	8.8	11.0	6.6	29.7
" "	"	12351	"	19.8	8.6	10.7	6.5	30.4
Alaska Peninsula	Recent	4358	M.V.Z.	24.4	11.0	12.9	8.3	36.8
California	"	22120	"	20.0	8.3	11.1	6.3	30.3
Mackenzie	"	137051	U.S.N.M.	20.0	9.2	10.5	6.7	29.8

Locality	Geologic age	Catalogue No.	Collection	Anterior, alveolar border of canine to posterior crown border of $M_1^1$	Breadth of $M_1^1$	Length of $M_1^1$	Outside length of $P_4^1$	Length of $P_2^1$	Breadth of $P_2^1$	Breadth across upper carnassials
Cumberland Cave	Pleistocene	8194	U.S.N.M.	49.8	12.5	7.2	18.3	.....	6.3	.....
" "	"	8215	"	50.5	13.0	6.9	18.6	9.2	6.0	60.9
" "	"	8176	"	53.3	.....	.....	19.1	9.2	6.1	58.7
22 specimens	Recent	maximum	M.V.Z.	56.2	14.7	8.3	23.6	11.0	7.1	71.5
"	"	minimum	"	47.3	12.3	6.6	17.7	9.4	5.3	58.2

There is the possibility that the Recent wolverine of the eastern United States is a smaller animal than the more western and northwestern animals here principally relied upon in making comparisons with the fossil form. In that event, the size difference between fossil and living forms might be less than our measurements indicate. However, the measurements of the two specimens from more eastern points, one from Minnesota and one from Quebec, do not reveal any trend toward smaller size of Recent animal in the eastern part of the continent.

It is in order here to say that no attempt has been made to apply to Recent specimens of *Gulo* the names proposed by Elliott (1903, p. 260; 1905, p. 81) and by Matschie (1918, pp. 148-153). Though it would be expected, on



geographic grounds, that some of these names would apply to certain Recent specimens used in the present comparison, the Recent material shows a homogeneity as regards size, and shape of P<sub>3</sub>, that permits its use as a unit in a comparison with the smaller Pleistocene animal. The cursory comparisons made of Recent specimens indicate that the names proposed by Elliot (*loc. cit.*) and by Matschie (*loc. cit.*), if valid, are at most of sub-specific rank. That is to say, if there are geographic variants to which these names may be applied, it is judged that the variants are connected by intergrades in the intervening geographic areas.

If one should treat the Pleistocene animals as a subspecies of the Recent species *Gulo luscus*, one would imply, of course, an ancestral position to *G. gidleyi*. Actually, the decision to treat *gidleyi* as a species rather than a subspecies was made because the degree of difference between it and any other described form of *Gulo* is thought to be greater than that between any two of the named forms of the living North American wolverine, and not because any decision was arrived at concerning the ancestral position of *gidleyi*. In so far as its morphological features are concerned, *gidleyi* may have given rise to Recent forms, but I am not prepared to prove that it did so.

The name *Gulo gidleyi* is proposed in memory of the late James W. Gidley, who was principally responsible for gathering the collection of Pleistocene vertebrates from Cumberland Cave.

#### Genus MARTES Pinel

Pinel, Actes Soc. Hist. Nat. Paris, vol. 1, p. 55. 1792.

*Diagnosis*—Skull ranging in basilar length from 60 to 115 mm.; facial angle slight; tympanic bullæ moderately inflated but not in close contact with paroccipital processes; palate behind last upper molars; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{4}{4} \frac{1}{2}$ ; inner moiety of M<sub>1</sub> larger than outer; P<sub>4</sub> with simple deutercone; in M<sub>1</sub> trigonid longer than talonid, metaconid small and appressed to protoconid, hypoconid large, talonid semibasined.

*Genotype*—*Martes domestica* Pinel = *Mustela foina* Erxleben.

*Remarks*—The living species and subspecies of the genus *Martes* in North America have been assigned to two subgenera, *Martes* and *Pekania*. *Pekania* Gray 1865 includes the Fisher, *Martes pennanti*, restricted to the Boreal zones of North America. The true martens are placed in the subgenus *Martes* Pinel. Critical study of the described species and subspecies of true martens (subgenus *Martes*) in North America almost certainly would show that the named forms belong to no more than two, and possibly to only one, full species.

The recording by Stock (1929, p. 285) of *Martes* from Rancho La Brea seems to have resulted from a confusion of names. Probably the name referred to long-tailed weasels of the genus *Mustela* then currently known as *Mustela xanthogenys xanthogenys* Gray. The same animal, by way of Stock's (*loc. cit.*) name, probably constituted basis for Osborn's ascription (1925, p. 531) of "*Mustela*, a species of the living marten" to the Rancho La Brea fauna.

#### *Martes americana americana* (Turton)

*Mustela americana*, Allen (1876, p. 333); Hay (1902, p. 767).

*Martes americana*, Hay (1930, p. 527).

*Remarks*—The sole basis for ascription to the Pleistocene seems to be Allen's (1876, p. 333) statement made relative to *Mephitis frontata* that ". . . a pretty careful examination of the fossil remains of *Carnivora*, col-

lected by Professor Baird many years since from the bone-caves of Pennsylvania (of which this fossil skull of the skunk forms a part), has failed to show any of them to be specifically different from the species now or recently living in the same region. Many of them are remains of individuals of large size, but not exceeding the dimensions of specimens of the recent animal from the same or contiguous regions. These remains include, among others, the following species: *Lynx rufus*, *Urocyon virginianus*, *Mustela pennanti*, *Mustela americana*, *Putorius vison*, *Lutra canadensis*, *Mephitis mephitis* (other specimens than the 'frontata skull'), *Procyon lotor*, *Ursus americanus*, etc." Whether or not these remains really are of Pleistocene age, or instead were deposited in the Recent, I do not know.

*Martes caurina sierræ* Grinnell and Storer

*Mustela* sp., Furlong (1904, p. 55; 1906, p. 245); Miller, L. H. (1912, p. 73); Stock (1918, p. 469).

*Mustela caurina nobilis* Hall (1926, p. 127, pl. 14); Hay (1927, pp. 214-215; 1930, p. 527).

*Remarks*—In 1926 the present writer described material from Samwel and Potter Creek caves of Shasta County, California, and made it the basis of the new name *Martes caurina nobilis*. Intensive study and comparison of measurements of the fossil specimens with measurements of corresponding parts of other described North American species and subspecies of martens, clearly showed that the fossil remains had closest relationship with *Martes caurina sierræ*. However, with 19 skulls of *M. c. sierræ* for comparison it was found that the two largest of the fossil specimens differed from the largest of the specimens of the Recent *M. c. sierræ* in larger size of teeth, more crowded premolars, deeper horizontal ramus of mandible and greater anteroposterior extent of coronoid process.

These differences now are not regarded as certainly of taxonomic worth. In the first place the greater depth of horizontal ramus and greater anteroposterior extent of coronoid process seem to be what one would expect if Huxley's (1932) law of simple heterogony applies. Although conformance with this law does not disprove the taxonomic worth of these differences, some doubt is cast by it. The other consideration, which did not occur to me in 1926, is that trapping for fur has reduced the average age of the Recent population of *Martes caurina sierræ* and that probably as a result of this the available series of nineteen individuals contains no animals as old as the oldest in the lot of approximately six cave specimens. The latter represent a population almost certainly not subjected to a similar age-reducing factor. Then, too, very young, and very old animals, the writer believes, tend to leave their remains in certain types of deposits, including caves, in greater proportion than do animals of intermediate ages. These considerations induce me now to place the name *Martes caurina nobilis* Hall, 1926, in the synonymy of *Martes caurina sierræ* Grinnell and Storer, 1916.

For a full discussion of the Pleistocene material, known only from Samwel and Potter Creek caves, Shasta County, California, reference may be made to Hall (1926).

*Martes pennanti* (Erxleben)

*Mustela pennanti*, Allen (1876, p. 333); Hay (1902, p. 767); Brown (1908, pp. 179-180); Osborn (1910, p. 488); Matthew (1915, p. 402).

*Martes pennanti*, Hay (1914, p. 32; 1924, p. 252; 1930, p. 527).

*Remarks*—J. A. Allen (1876, p. 333) mentions having examined material of this species from caves in Pennsylvania. The other occurrence ascribed to the Pleistocene is that at Conard Fissure, Arkansas, first reported by



Brown (1908, p. 179). Four lower jaws, the left anterior portion of a skull, and two separate teeth, a lower sectorial and an upper carnassial, were found. The present writer has not examined the material but judging from the small size as recorded by Brown for the one adult specimen it was a female, or possibly a male of *Martes diluviana*.

This occurrence at Conard Fissure during the Pleistocene is especially noteworthy because the subgenus *Pekania* now does not range nearly that far south. A western subspecies of *Mustela pennanti* has been named by Rhoads (Trans. Am. Philos. Soc., 19, 435) but is here not recognized because I have inadequate material from eastern North America to reveal differences, if such exist, between western and eastern animals.

#### *Martes diluviana* (Cope)

*Mustela diluviana* Cope (1899, pp. 228-229, pl. 18, figs. 5, 5a); Schlosser (1902, p. 141); Hay (1902, p. 767); Rhoads (1903, p. 229); Trouessart (1904, p. 204); Baker (1920, pp. 215, 397); Hay (1923, p. 312; 1930, p. 528).

*Martes parapennanti* Gidley and Gazin (1933, pp. 347-349, fig. 2).  
martens, Gidley (1920, p. 283).

*Martes diluviana*, Hall (1926, p. 130); Gidley and Gazin (1933, p. 349).

*Type*—No. 65, Academy of Natural Sciences of Philadelphia. A fragment of left lower jaw figured by Cope (1899, pl. 18, fig. 5a) and an isolated left M1. Each bears the number 65. Whether one of these two specimens, or instead one of the two others available to Cope but not seen by the present writer, constitutes the actual type-specimen is an open question.

*Diagnosis*—Resembling *Martes pennanti* but size averaging an eighth less in linear dimensions of teeth.

*Remarks*—Of Cope's original material, four lower jaws, I have examined two specimens, the crown of a left M1 and a fragment of a left lower jaw bearing M1, the alveoli of P3, P4 and M2. The latter specimen is the one shown in Cope's figure 5a of plate 18 (1899). A third specimen is shown in his figure 5 of the same plate. Of the fourth specimen I have no knowledge beyond the mere mention made of it by Cope (*op. cit.*, p. 229).

The species *Mustela diluviana* originally was characterized as intermediate in size between *M. pennanti* and *M. americana* and as differing from *M. americana* and agreeing with *M. pennanti* and *M. martes* in the full development of the metaconid on M1 and "in the absence of posterior median lobe on the pm2" [now currently designated as P3].

After having taken four different measurements on M1 of 40 female and 40 male skulls of *Martes americana*, of several subspecies, representing both sides of the continent, it is clear that the smallest M1 of *M. diluviana* is larger than the largest M1 of the male marten.

However, corresponding measurements of 54 *M. pennanti*, about half of which are females, show that of the three specimens of *M. diluviana*, known to me (one known only from Cope's figure, *loc. cit.*) from the Port Kennedy bone deposit, two are no smaller than some females of the Recent fisher. Also, it may be added that neither of the two specimens of *M. diluviana* examined, nor the third one which is figured (*op. cit.*, fig. 5) presents any differences from *M. pennanti* in relative proportions. The slight spacing of the premolars which Cope (*op. cit.*, p. 229, pl. 18, fig. 5) thought differentiated the Pleistocene animal from the Recent *M. pennanti* is not constantly distinctive since some of the smaller, though fully adult, females of *pennanti* have each premolar actually touching the tooth behind it. The absence of an accessory cusp on P3 of *M. pennanti* is not a constant char-



acter. Indeed, in the specimens which I have examined this cusp is more often present than absent, though it is likely to disappear early in life as a result of wear.

Thus, there remains as distinctive of *M. diluviana*, the size of the first lower molar which, in one of the three specimens, is less than in any specimen seen of *M. pennanti*. Perhaps the two larger specimens of *diluviana* are males and the third specimen, in which M1 is smaller than in any Recent female of *M. pennanti*, is a female of normal size for the species *diluviana*.

With only 20 male and 15 female skulls of *M. pennanti*, all save one from western North America, available for comparison, it was suspected that females from eastern North America might prove to have teeth as small as the specimens from the Port Kennedy bone deposit. This suspicion now seems less justified, for Dr. C. L. Gazin has furnished me with measurements taken by him of the teeth of 18 additional specimens, in the United States National Museum, all from eastern North America, without finding any bearing teeth as small as the smallest teeth from Port Kennedy.

Since writing the above I have examined casts of some of the specimens of *Martes* from Cumberland Cave of Maryland described by Gidley and Gazin (1933, p. 347). The smaller of these specimens, like some of those from the Port Kennedy bone deposit, are of lesser size than the smallest Recent specimens. Employing individuals of the same sex it is found that the fossil animal averages 12.5 (7-18) per cent smaller in linear dimensions of teeth. This is roughly the same amount of difference found (see Hall, 1934, p. 367) between the sexes of *M. pennanti*. Accordingly the male of the fossil animal, at least in linear dimensions of teeth, was about the size of the female of the living fisher.

Gidley and Gazin (1933, pp. 347-349) describe their fossil specimens from Cumberland Cave as differing from Recent *M. pennanti* in the following respects. Size less; P4 relatively shorter with protocone more forward in position; external roots of M1 less distinctly separated; modifications (depth of masseteric fossa and its division into two distinct fossæ) of coronoid region more pronounced; condyle of lower jaw shallower. By using Recent specimens of *M. pennanti* not seen by these authors, I have verified to my own satisfaction the size difference. How many of the remaining differences would be represented by individual, age, and secondary sexual variation in the specimens available to me I do not know. The outside length of P4, relative to the distance between the anterior border of the crown of P2 and the posterior border of the crown of the outer moiety of M1, is found to be exactly the same in certain Recent specimens as in their type specimen. The other comparative differences mentioned by them would require for reappraisal direct comparison of the actual specimens which at the moment are not available. At any rate, on the basis of size alone, I have satisfied myself of the specific distinctness of *M. pennanti* and the animal from Cumberland Cave.

In proposing the name *Martes parapennanti* for the Cumberland Cave animal Gidley and Gazin thought it specifically different from *Martes diluviana* by reason of the deeper horizontal ramus of the mandible and the smaller metaconid on M1. The metaconid of the specimen that I examined from Port Kennedy is no better developed than in the cast of No. 11,877 from Cumberland Cave, if allowance is made for greater wear to which the latter obviously was subjected.

Comparison with Recent specimens of *Martes pennanti* reveals that the shallowness of the mandibular ramus of the Port Kennedy specimen exam-

ined by me, and figured by Cope (1899, pl. 18, fig. 5a) is, at least in part, the result of immaturity. The porous nature of the bone, the unworn  $M\bar{I}$  and the open character of the alveoli clearly identify the specimen as immature. In *Martes pennanti* the mandible increases in depth with increasing age. However, the second specimen figured by Cope (1899, pl. 18, fig. 5), and incidentally not examined by me, also has a shallow horizontal ramus. From the figure alone I can not form a reliable estimate of the age of the animal, though the sharp outlines of  $M\bar{I}$  indicate that it was not of an old animal. If it, too, belonged to a young animal, the difference between it and the deeper jawed adults figured (Gidley and Gazin, 1933, fig. 2) from Cumberland Cave are explicable as age differences. If, on the other hand,

*Measurements in millimeters of  $M\bar{I}$  of Martes diluviana and females of Martes pennanti*

Collection	Catalogue No.	Species	Locality	Length	Length of trigonid from notch	Length of trigonid from posterior border of protoconid	Breadth of talonid
U.S.N.M.....	81214	<i>M. pennanti</i>	Godbout, Quebec	11.5	....	....	....
M.V.Z.....	43621	"	Indian Point Lake, B. C.	12.7	9.5	8.8	4.3
" .....	44543	"	"	12.3	9.0	8.5	4.3
" .....	43614	"	"	12.6	9.3	8.6	4.7
" .....	29813	"	Yosemite Park, Calif.	12.0	8.9	8.4	4.6
" .....	20955	"	Mendocino Co., Calif.	11.7	8.7	8.0	4.1
" .....	36641	"	Oxford Co., Maine	12.2	9.0	8.3	4.6
Acad. Nat. Sci. Phila.	65	<i>M. diluviana</i>	Port Kennedy, Penn.	10.8	7.8	7.0	3.9
" .....	65	<i>M. diluviana</i>	"	12.4	8.7	8.3	4.7

this lower jaw from the Port Kennedy bone deposit is that of an adult, the difference in depth of ramus between it and the Cumberland Cave specimens might still be individual variation in a single species. Among eight males of *M. pennanti* from the Bowron Lake region of British Columbia, I find a very old male in which the depth of jaw, taken on the outside, below the heel of  $M\bar{I}$  equals 107 per cent of the length of  $M\bar{I}$ , whereas in a subadult male the percentage is only 86.4, making a difference of 20.6 per cent. Among 14 females from the same place there is a variation of 18.2 (94.3 to 76.1) per cent. In the Cumberland Cave fossil, No. 11,877, the depth of the mandible is 99.3 per cent and in the specimen from Port Kennedy (according to Cope's illustration) 86.6 per cent. This is a variation of only 12.7 per cent as opposed to one of 20.6 per cent found among 8 males of the Recent *M. pennanti* from a single locality. It is felt, therefore, that *Martes parapennanti* has not been shown to be distinct from *Martes diluviana* and that the former name should be treated as a synonym of the latter.

#### Genus MUSTELA Linnæus

Linnæus, Syst. Nat., ed. 10, vol. 1, p. 45.

*Diagnosis*—Skull ranging in basilar length from 16 to 70 mm.; facial angle slight; tympanic bullæ greatly inflated (moderately in *Lutreola*), cancellous, and with paroccipital processes closely appressed; palate behind upper



molars; dental formula:  $\frac{3}{3} \frac{1}{1} \frac{3}{3-2} \frac{1}{2}$ ; inner moiety of  $M_1$  larger than outer;  $P_4$  with simple deutocone; in  $M_1$  trigonid longer than talonid, metaconid absent, talonid trenchant.

*Genotype*—*Mustela erminea* Linnæus.

*Remarks*—In North America the genus *Mustela* has three subgenera. One of these, *Putorius*, is represented by the single species *Mustela nigripes*, the black-footed ferret. This species has not been divided into geographic races and no fossil remains of it are known. However, fossil remains of the other two subgenera are known.

Of *Lutreola*, comprising the minks, fossil or sub-fossil remains are available from four localities. One extinct species is known and the living forms to which most of the fossil remains are referred are members of a single species, satisfactorily treated systematically by Hollister (1913). His arrangement is modified only by the change of name (see Hollister, 1914) for one race and the addition of two other races named since 1913 (see Grinnell, 1916, p. 213, and Hall, 1932, p. 418).

The subgenus *Mustela*, true weasels, however, is less well known and the writer's as yet uncompleted study of it prevents offering here a satisfactory systematic arrangement of all members of the group. Nevertheless, study has been made of the long-tailed forms, to which group most of the fossil remains pertain and the preliminary descriptions of new forms and revised list offered below will permit proper allocation of the Pleistocene materials.

It is in order here to point out that American weasels of the subgenus *Mustela* fall into three groups, the least weasels represented by *Mustela rixosa* (Bangs), the short-tailed weasels represented by *Mustela cicognanii* Bonaparte, and the long-tailed weasels of which *Mustela frenata* Lichtenstein is an example. Members of the last-mentioned group currently have been treated as comprising 33 recognizable forms (species and subspecies) belonging to 22 full species. As a result of the studies now being reported upon, it is found that there are only two full species in the long-tailed weasel group, one of which has two geographic races, or subspecies, and the other comprising 42 subspecies, making a total of 44 kinds.

In the following accounts, color terminology, unless otherwise stated, is that of Ridgway: Color Standards and Color Nomenclature, 1912. Linear measurements are in millimeters and weights are in grams.

## DESCRIPTIONS OF NEW SUBSPECIES

### *Mustela frenata nevadensis* new subspecies

*Type*—Female, adult, skull and skin; No. 41503, Mus. Vert. Zool.; three miles east of Baker, White Pine County, Nevada; May 30, 1929; collected by E. R. Hall and W. C. Russell; original No. 2674, E. R. H.

*Range*—Altitudinally, 700 feet at Wenatchee, Washington, to the highest parts of the mountains of western United States; Upper Sonoran Zone to Arctic-Alpine Zone; southern British Columbia in the Cascades and territory west to Monashee Mountains and Nelson; southward in the Cascades of northern Washington; over western Washington, Idaho, Utah and Nevada to northeastern Arizona and northern New Mexico; westward from the eastern base of the Rocky Mountains in Colorado to the western base of the Sierra Nevada and Cascades of California, and to the Cascades of southern Oregon.



*Diagnosis*—Size: Medium (see measurements). Color: Upperparts in summer near (14 *n* to *l*) Brussels brown or tones 1 to 3 of raw umber of Oberthür and Dauthenay, pl. 301 (*Répertoire de Couleurs*, Paris, Librairie horticole, 1905); top of head darker from nose to line connecting posterior margins of ears; chin and upper lips white; remainder of underparts buff yellow to straw yellow and sometimes ochraceous buff, especially in young and in some adults from southern Colorado; in winter all white, except tip of tail which is at all times black, or upperparts near (*j*) snuff brown or lighter than Brussels brown with a smoked effect and underparts white; color of underparts extends distally on posterior sides of fore limbs over toes onto antipalmar faces of feet and wrists, on medial sides of hind limbs to ankles, over antiplantar faces of toes, medial third of tarsus and usually over proximal tenth to three-fourths of ventral side of tail; least width of color of underparts averaging, in a series of 20 males from the southern half of the Sierra Nevada of California, 59 (37–76) per cent of greatest width of color of upperparts. In seven males from southern Colorado corresponding percentages are 55 (37–71). Black tip of tail in series from Sierra Nevada averaging 50 (40–60) mm. long; thus longer than hind foot and averaging  $33\frac{1}{3}$  per cent of length of tail vertebrae. Skull and teeth: Male (based on 25 adults from Sierra Nevada of California): See measurements; weight, 3.7 (2.9–4.9) grams; basilar length 43.6 (40.6–46.1); zygomatic breadth more than distance between condylar foramen and  $M_1$  (save in four specimens) and more than distance between anterior palatine foramen and anterior margin of tympanic bulla (save in 2 specimens); mastoid breadth more (80 per cent) or less (20 per cent) than postpalatal length; postorbital breadth less than combined length of upper premolars and more or less than width of basioccipital measured from medial margin of one foramen lacerum posterior to its opposite; interorbital breadth more or less than distance between foramen opticum and anterior margin of tympanic bulla; breadth of rostrum less than length of tympanic bulla; least width of palate less than medial length of  $P_4$  (save in two specimens); anterior margin of tympanic bulla as far posterior to foramen ovale as combined width of 3 to 5 (including  $I_3$ ) upper incisors; height of tympanic bulla more than distance from its anterior margin to foramen ovale; length of tympanic bulla more than length of lower molar and premolar tooth-row and longer or shorter than rostrum (as measured from posterior base of postorbital process of frontal to anterior end of nasal); anterior margin of masseteric fossa not carried farther forward than point directly below hypoconid of  $M_1$ . Female (based on 10 adults from Sierra Nevada of California): See measurements; weight, 2.2 (1.8–2.4) grams; basilar length, 38.2 (36.7–39.5); zygomatic breadth more (save in one specimen) than distance between condylar foramen and  $M_1$  and more (save in 2 specimens) than distance between anterior palatine foramen and anterior margin of tympanic bulla; postorbital breadth less than combined length of upper premolars and (save in one specimen) less than width of basioccipital measured from medial margin of one foramen lacerum posterior to its opposite; least width of palate more or less than either outside or inside length of  $P_4$  but generally less than inside length; tympanic bulla as far posterior to foramen ovale as combined width of 3 to  $5\frac{1}{2}$  (including  $I_3$ ) upper incisors; height of tympanic bulla more or less (usually more) than distance from its anterior margin to foramen ovale; length of tympanic bulla more than length of lower molar-premolar tooth-row and more or less than length of rostrum.

The skull of the female averages 41 per cent lighter in weight than that of the average male.

Compared with the skull of *M. f. arizonensis* that of *nevadensis* is larger, more heavily ridged and has less inflated tympanic bullæ and a relatively smaller mastoid breadth.

*Remarks*—The populations here assigned to *nevadensis* have been called *arizonensis* since Mearns proposed this name in 1891. However, study of the now more adequate material shows that true *arizonensis* is a much smaller animal with a differently proportioned skull.

*Specimens examined*—Total number, 392. Marginal localities by states are as follows: *British Columbia*: Nelson; Sicamous; Hope-Princeton Summit, 5600 feet. *Washington*: Barron, 5000 feet, Whatcom County; Easton, Kittitas County. *Oregon*: Riverside, Malheur County; Burns, Harney County; 20 miles W Crescent, Klamath County; Anna Creek, Mount Mazama, Klamath County. *California*: Hornbrook, Siskiyou County; Mount Shasta, Siskiyou County; Kelly's, 2 miles S Williw Lake, 5200 feet, Plumas County; Quincy, Plumas County; Blue Cañon, 5000 feet, Placer County; Wawona, Mariposa County; E fork Kaweah River, 9800 feet, Tulare County. *Nevada*: Arlemont, 4850 feet, Fish Lake Valley, Esmeralda County; 3 miles S Crystal Spring, 3900 feet, Pahrnagat Valley, Lincoln County. *Utah*: St. George, Washington County. *Arizona*: 15 miles E Luka Chu Kai Navajo School, 8000 feet, Apache County. *New Mexico*: Taos, Taos County; Ribera, San Miguel County. *Colorado*: Osier, Conejos County; Villagrove, Saguache County; Colorado Springs, 6000 feet, El Paso County; Barr, Adams County. *Wyoming*: Buffalo, Johnson County; Yellowstone Lake, Yellowstone National Park. *Idaho*: Dry Creek, Targee National Forest, Clark County; Leadore, Lemhi County; Locksa River, Idaho County.

*Mustela frenata effera* new subspecies

*Type*—Male, adult, skull and skin; No. 33637, Amer. Mus. Nat. Hist.; Ironside, 4000 feet, Malheur County, Oregon; September 8, 1912; collected by H. E. Anthony; original No. 267.

*Range*—Upper Sonoran to Arctic-Alpine zones of northern two-thirds of Oregon east of the Cascades and southeastern Washington, south of the Snake River.

*Diagnosis*—Size: Small (see measurements). Color: As described in *Mustela frenata nevadensis*. Skull and teeth: Male (based on 6 adults from northeastern Oregon): See measurements. As described in *M. f. nevadensis* except that weight 2.9 (2.5–3.4) grams; basilar length, 40.5 (39.3–41.8). Female (based on No. 212423, U. S. Nat. Mus., from Vale): In so far as parts of the broken skull permit one to judge, it is as described in *M. f. nevadensis* except for the following characters: smaller; lighter; post-orbital breadth more than width of basioccipital measured from medial margin of one foramen lacerum posterior to its opposite.

*Remarks*—This geographic race has long gone by the name *Mustela arizonensis* (Mearns), which it does resemble in coloration and small size. However, its skull is differently proportioned. For one thing the tympanic bullæ are less inflated. From *M. f. nevadensis*, *effera* differs principally in smaller size, averaging about 8 per cent smaller in linear measurements of the skull and 22 per cent lighter. Also the male skull of *effera* seems, on the average, to have the preorbital part of the skull smaller. Males average 12.5 per cent smaller than *nevadensis* in external measurements.



*M. f. effera* reaches its extreme of small size in the Blue Mountain region of northeastern Oregon. Complete intergradation with each adjoining subspecies is indicated by numerous specimens.

*Specimens examined*—Total number, 49, from localities as follows: OREGON, by counties from north to south, as follows: *Wasco County*: Wapinitia, 1, Antelope, 2; 7 miles E Antelope, 5. *Gilliam County*: Condon, 1. *Morrow County*: 10 miles S Hardman, 1. *Umatilla County*: Umatilla, 1. *Union County*: Elgin, 1; 20 miles E Lehman, 1. *Wallowa County*: Horse Creek, 15 miles N Paradise, 1; Enterprise, 1; Wallowa Lake, 1; Wallowa Mts., 8300 feet, 1. *Baker County*: Anthony, 3; Bourne, 2. *Grant County*: Long Creek, 1; Canyon Creek, 1; Strawberry Mts., 2; Silvies, 1. *Crook County*: Prineville, 4. *Deschutes County*: Sisters, 2; Bend, 1. *Lake County*: 3 miles W Stauffer, 1; Fort Rock, 1. *Harney County*: 25 miles NW Burns, 1. *Malheur County*: 4000 feet, Ironside, 2; 1½ miles S Vale, 2. WASHINGTON: *Walla Walla County*: Prescott, 4; Ft. Walla Walla, 2; Wallula, 1. *Asotin County*: Asotin, 1.

*Mustela frenata altifrontalis* new subspecies

*Type*—Male, adult, skull and skin; No. 42093, Mus. Vert. Zool.; Tillamook, Tillamook County, Oregon; July 10, 1928; collected by Alex Walker; original No. 717.

*Range*—Altitudinally from sea-level up to at least 4800 feet (Mount Baker) principally in the Transition Zone of the humid coastal region of Oregon, Washington, and extreme southwestern British Columbia.

*Diagnosis*—Size: Medium (see measurements). Color: Upperparts, in summer, near (*n*) argus brown or tone 4 of brownish drab of Oberthür and Dauthenay, pl. 302; dark spot at each angle of mouth well developed, often fused with color of upperparts which sometimes covers lower lips; chin white; remainder of underparts near (14'a to 16'c) ochraceous buff. In winter upperparts near (14) argus brown with smoked effect and warm buff to Naples yellow below; tip of tail at all times black; color of underparts extends distally on posterior sides of fore limbs over toes onto antipalmar faces of feet and usually all of wrists, on medial sides of hind limbs typically only to knee, but sometimes to ankle; tips of toes on hind feet almost always marked with color of underparts; least width of color of underparts averaging, in a series of 14 males from Blaine, Oregon, 23 (14–36) per cent of greatest width of color of upperparts. Black tip of tail in 8 adult males from Blaine, Oregon, averaging 59 (47–70) mm. long; thus longer than hind foot and averaging 37 per cent of length of tail vertebræ. Skull and teeth: Male (based on 9 adults from Blaine, Tillamook County, Oregon): See measurements. As described in *Mustela frenata nevadensis* except that: weight, 4.4 (3.3–5.3) grams; basilar length, 45.6 (42.4–47.7). Female (based on 4 adults from Oregon): See measurements. As described in *M. f. nevadensis* except that zygomatic breadth more or less (less in 3 of 4) than distance between condylar foramen and M1 or than between anterior palatine foramen and anterior margin of tympanic bulla; least width of palate not less than greatest length of P4.

The skull of the female averages 50 per cent lighter than that of the male.

Compared with *M. f. nevadensis* the skull of the male of *altifrontalis* averages slightly larger and heavier though the skulls of females are of about the same size and weight. Relative to the basilar length both sexes are deeper through the braincase and narrower across the mastoids; the rostrum is broader, especially in males; the upper tooth-rows are shorter and the interorbital breadth less, especially in females.



*Remarks*—The animal here called *altifrontalis* has long gone by the name of *Mustela saturata* (Merriam). The latter name is now restricted to the long-tailed weasel found to the southeastward in northern California and southern Oregon and separated geographically from *altifrontalis* by the intervening subspecies *Mustela frenata oregonensis*. Specimens are available showing intergradation with each adjoining subspecies of *Mustela frenata*. For example, of four specimens recorded from British Columbia, only one, that from Chilliwack, is typical of *altifrontalis*. The other three are intergrades with *nevadensis*.

*Specimens examined*—Total number, 51, by localities from north to south as follows: BRITISH COLUMBIA: Chilliwack, 1; Lihumpton Park, 4750 feet, 2; Cultus Lake, 1. WASHINGTON: *Whatcom County*: Nooksack River, 2000 feet, 14 miles E Glacier, 1; Swamp Creek, 2050 feet, Nooksack River, 3; Lookout, 4800 feet, Mount Baker, 2. *Skagit County*: Rockport, 1. *King County*: 7 miles E Kent, 1. *Pierce County*: Tacoma, 1. *Clallam County*: Happy Lake, 1; Olympic Mountains, Elwha River, mouth of Boulder Creek, 560 feet, 1; Elwha River, Hume's Ranch, 560 feet, 1. *Mason County*: Lake Cushman, 2. OREGON: *Clatsop County*: Astoria, 1. *Tillamook County*: Tillamook, 12; Netarts, 1; Blaine, 16. *Lane County*: Reed, 1; Mercer, 1. *Curry County*: Langlois, 1.

*Mustela frenata nigriauris* new subspecies

*Type*—Male, adult, skeleton and skin; No. 70210, Mus. Vert. Zool.; 2½ miles E Santa Cruz, Santa Cruz County, California; March 11, 1936; collected by C. H. Russell; original No. 4225 of W. C. Russell.

*Range*—Altitudinally, sea-level to highest parts of Coast Range; Sonoran and Transition zones of Coast Range and coast of California from San Francisco Bay south to Point Conception, Santa Barbara County, California.

*Diagnosis*—Size: Medium (see measurements). Color: Spot between eyes, band confluent with color of underparts on each side of head extending anterodorsally anterior to each ear, and posterior third of each upper lip tinged with color of underparts or less often pure white; chin and lower lips white; remainder of sides and top of head posteriorly to or a little behind a line connecting posterior margins of ears, blackish; inside of pinna of ear and sometimes outside of pinna, blackish; dark spot posterior to each angle of mouth present on each side in three-fourths of specimens; tip of tail black; remainder of upperparts near (*l*) antique brown, and with more yellow than tone 3 of raw umber of Oberthür and Dauthenay, pl. 301. Often with more blackish and red in winter; tip of tail black; underparts near (*a* to *c*) ochraceous buff or orange salmon; ochraceous salmon in some juveniles; color of underparts extends distally on posterior sides of fore limbs over toes onto antipalmar faces of feet and wrists and on medial sides of hind limbs over antipalmar faces of toes; least width of color of underparts averaging, in 17 adult males (Berkeley, 5; San Francisco, 5; Palo Alto, 7), 55 (40–73) per cent of greatest width of color of upperparts. Black tip of tail in same series of males averaging 51 (35–60) mm.; thus averaging longer than hind foot and 33 per cent of length of tail vertebrae. Skull and teeth: Male (based on 6 adults from Palo Alto): See measurements; weight, 5.4 (5.0–5.9) grams; basilar length, 47.0 (46.1–48.1); zygomatic breadth more than distance between condylar foramen and M<sub>1</sub> or than between anterior palatine foramen and anterior margin of tympanic bulla; mastoid breadth more than postpalatal length; post-orbital breadth less than combined length of upper premolars (less than distance between posterior borders of P<sub>4</sub> and

P2) and less than width of basioccipital measured from medial margin of one foramen lacerum posterior to its opposite; interorbital breadth not greater than distance between foramen opticum and anterior margin of tympanic bulla; breadth of rostrum less than length of tympanic bulla; least width of palate less than outside length of P4; anterior margin of tympanic bulla as far posterior to foramen ovale as combined width of 3 or 4 (including I3) upper incisors; height of tympanic bulla more than distance from its anterior margin to foramen ovale; length of tympanic bulla more or less than (about equal to) length of lower molar and premolar tooth-row and longer or shorter (usually shorter) than rostrum; anterior margin of masseteric fossa below anterior half of M2. Female (based on 3 adults): See measurements; weight, 2.7 grams; basilar length, 41.2 (40.2–42.2); zygomatic breadth more or less than distance between condylar foramen and M1 or than distance between anterior palatine foramen and anterior margin of tympanic bulla; postorbital breadth less than combined length of upper premolars and less than width of basioccipital measured from medial margin of one foramen lacerum posterior to its opposite; least width of palate less than outside length of P4; tympanic bulla as far posterior to foramen ovale as combined width of 3 (including I3) upper incisors; height of tympanic bulla more than distance from its anterior margin to foramen ovale; length of tympanic bulla more than length of lower molar and premolar tooth-row and longer or shorter than rostrum.

The female skull is 50 per cent lighter than that of the average male.

*Remarks*—Intergrades with the race adjoining on the south are available and specimens from Los Baños, though typical *xanthogenys* in coloration, have larger, more angular skulls like those of *nigriauris*. From *M. f. munda* (Bangs) to the north of San Francisco Bay and Carquinez Straits *nigriauris* is sharply distinct on basis of color of the inside of the pinna of the ear. In *nigriauris* this is blackish like the darker facial markings but in *munda* the inside of the ear is colored like the back. Intergradation does not occur directly but probably through *M. f. xanthogenys*.

*Specimens examined*—Total number, 76, all from California, listed by counties from north to south, as follows: *Contra Costa County*: Glen Frazer Station, 1; 2 miles W Pinole, 1; Richmond, 1; 7 miles E Clayton, 1; Moraga Valley, 1; Concord, 1. *Alameda County*: Berkeley, 10; Oakland, 1; Piedmont, 1; Hayward, 2; near Hayward, 2; 10 miles E Hayward, 1; Redwood Canyon, 1. *San Francisco County*: San Francisco, 9; Ocean View, 1. *San Mateo County*: Moss Beach, 1; Half Moon Bay, 1; Redwood City, 1; Menlo Park, 7; no locality save county, 1. *Santa Clara County*: ¼ mile S Milpitas, 1; Leland Stanford Jr. University, 6; Palo Alto, 11. *Santa Cruz County*: 3 miles E Santa Cruz, 1; Santa Cruz, 4. *Monterey County*: Pacific Grove, 1; Monterey, 1; Carmel Valley, 1; Carmel, 1; Gonzales, 1. *San Luis Obispo County*: 5 miles SE Santa Margarita, 1; Morro, 1. *Kern County*: McKittrick asphalt deposit, 1. *Santa Barbara County*: Santa Maria, 1.

#### *Mustela frenata latirostra* new subspecies

*Type*—Male, adult, skull and skin; No. 3257, Mus. Vert. Zool.; San Diego, San Diego County, California; May 20, 1907; collected by Frank X. Holzner.

*Range*—Altitudinally sea-level to 8000 feet (Tahquitz Valley, San Jacinto Mts.); Sonoran and Transition zones of coast and mountains west of Mojave and Imperial deserts of southern California from Point Conception and Cuyama Valley southward to Mexican boundary.

*Diagnosis*—Size: Medium (see measurements). Color: As described in *Mustela frenata nigriauris*. Skull and teeth: Male (based on 6 adults from



San Diego County): See measurements. As described in *M. f. nigriauris* except that weight, 3.9 (3.8–4.0) grams; basilar length, 43.8 (41.9–47.0); postorbital breadth more than width of basioccipital measured from medial margin of one foramen lacerum posterior to its opposite; interorbital breadth not less than distance between foramen opticum and anterior margin of tympanic bulla; anterior margin of tympanic bulla as far posterior to foramen ovale as combined width of 2 to  $2\frac{1}{2}$  (including I3) upper incisors; length of tympanic bulla more than length of lower molar and premolar tooth-row and longer than rostrum; anterior margin of masseteric fossa below M2. Female (based on 4 adults from San Diego County): See measurements. As described in *M. f. nigriauris* except that: Weight, 2.6 (2.2–2.8) grams; basilar length, 40.0 and 40.1; postorbital breadth more than width of basioccipital measured from medial margin of one foramen lacerum posterior to its opposite; length of tympanic bulla more than length of rostrum.

The female skull averages 34 per cent lighter than that of the average male.

Compared with the skull of *M. f. nigriauris*, both males and females of *latirostra* have a generally smaller skull in which the interorbital and postorbital regions are smaller and the tympanic bullæ relatively larger and more inflated.

*Remarks*—This subspecies, together with others, long has gone by the name *Mustela xanthogenys* Gray and the type locality was generally supposed to be in the vicinity of San Diego. This supposition seems to have originated with Merriam's (North Amer. Fauna, No. 11, p. 25, 1896) statement that the type locality was "southern California, probably vicinity of San Diego." However, when Gray named the species, and when referring to it in later accounts, he never defined the locality whence the type specimen came more definitely than "California." The type specimen was obtained during the course of the voyage of the British ship *Sulphur* under the command of Sir Edward Belcher.

Examination of Belcher's "Narrative of a voyage round the world performed in her majesty's ship *Sulphur* . . ." (London, 1843) indicates that weasels might have been obtained in California from places within the ranges as now known of *Mustela frenata latirostra*, *M. f. nigriauris*, *M. f. munda* and *M. f. xanthogenys*. However, Mr. Reginald I. Pocock's comparison of the type specimen in the British Museum with several California-taken specimens sent him shows that the skull of the type is larger than that of *latirostra* and that the skin of the type lacks the blackish color of the head which causes the inside of the pinna of the ear to be blackish in *latirostra* and *nigriauris*. In this respect the type specimen agrees with animals from north of San Francisco Bay and those from the San Joaquin and Sacramento valleys. Accordingly the name *xanthogenys* would seem to apply to one of the two races here called *munda* and *xanthogenys*—to which one, only additional comparisons with the type specimen will determine. However, the fact that relatively little opportunity was had to obtain the type specimen from the range now assigned to *munda*, and Belcher's (*op. cit.*, vol. 1, p. 129) statement that a weasel was taken on their trip up the Sacramento River to as far as Point Victoria, lat.  $38^{\circ}46'47''$  north, and return to San Francisco Bay, favors the possibility that the type specimen came from the interior valley region of California, and it is to the light-colored animal of these interior valleys that the name *xanthogenys* seems best applied.

*Specimens examined*—Total number, 133, all from California, listed by counties from north to south as follows: *Santa Barbara County*: Carpinteria asphalt deposit, 1. *Ventura County*: Cuyama Valley, 2200 feet, 1; Nord-



hoff, 3; Ventura, 7. *Los Angeles County*: near Owensmouth, 1; Cahuenga, 1; Flint Ridge, Pasadena, 1; Pasadena, 3; Lankershim, 1; 1 mile S Lankershim, 1; Duarte, 1; Covina, 1; Claremont, 1; El Monte, 4; Montebello, 1; Alhambra, 6; El Nogal, 2; Rancho La Brea asphalt pits, 57. *San Bernardino County*: San Bernardino, 4; San Bernardino Valley, 1; Redlands, 2; Bluff Lake, San Bernardino Mountains, 2. *Riverside County*: West Riverside, 1; Banning, 1; Cabazon, 1; San Jacinto Plain, 1; Tahquitz Valley, 8000 feet, 1; Elsinore, 1. *San Diego County*: Twin Oaks, 1; San Marcos, 2; Witch Creek, 1; Ballena, 1; Santa Ysabel, 3; Julian, 1; La Jolla, 1; Lakeside, 1; El Cajon, 1; San Diego, 9; Jamaca, 2; Chula Vista, 1; El Vido (not found), 1.

*Mustela frenata pulchra* new subspecies

*Type*—Male, adult, skeleton and skin, No. 16668, Mus. Vert. Zool.; Buttonwillow, Kern County, California; April 30, 1912; collected by J. Grinnell; original No. 1953.

*Range*—Altitudinally, about 300 feet in San Joaquin Valley to 2500 feet, Isabella; Upper and Lower Sonoran zones of southern end of San Joaquin Valley and in mountains at southern end of Valley, California.

*Diagnosis*—Size: Large (see measurements). Color: Spot between eyes, band confluent with color of underparts, on each side of head extending anterodorsally anterior to each ear, posterior third of each upper lip, lower lips, and chin, white or more often darker than ochraceous buff and therefore same color as belly; dark spot posterior to each angle of mouth present but small; tip of tail black; remainder of upperparts near (16j) buckthorn brown to near (h) yellow ocher and from tone 2 to 4 of brown pink of Oberthür and Dauthenay, pl. 297, but with a trifle more reddish brown; upperparts of uniform color except for occasional slight darkening of nose, forehead and areas around eyes; underparts darker (a) than ochraceous buff; color of underparts extends distally on posterior sides of fore limbs over toes onto antipalmar faces of feet and wrists, on medial sides of hind limbs over antipalmar faces of toes, tarsal region and sometimes in diluted fashion on proximal third of underside of tail; least width of color of underparts averaging, in 6 male topotypes, 55 (43–81) per cent of greatest width of color of upperparts. Black tip of tail in same series of males averaging 58 (53–63) mm. long; thus averaging longer than hind foot and 33 per cent of length of tail vertebræ. Skull and teeth: Male (based on 6 adults; type and 5 topotypes): See measurements. As described in *M. f. nigriauris* except that: weight, 5.3 (4.5–6.1) grams; basilar length, 47.6 (46.0–48.6); inter-orbital breadth more or less than distance between foramen opticum and anterior margin of tympanic bulla; anterior margin of tympanic bulla as far posterior to foramen ovale as combined width of 2 to 3½ (including 13) upper incisors; length of tympanic bulla more than length of lower molar and premolar tooth-row and shorter than rostrum. Female: typical adult not seen.

Compared with skulls of male *latirostra*, that of *pulchra* is more than one-fourth heavier; has a deeper braincase, and measures larger in basilar length, orbitonasal length, zygomatic breadth, and mastoid breadth. Also the tympanic bulla is shorter than the rostrum (as measured from the posterior base of the postorbital process to the anterior end of the nasals) whereas the reverse is true in *latirostra*.

*Remarks*—A skin-only, No. 16270, Mus. Vert. Zool., from Isabella, was made up from a badly decayed animal and is only tentatively referred to *pulchra*. The most that can be told from the specimen is that it is a

relatively light colored, bridled weasel. The fact that the color is slightly darker than in *pulchra* may or may not indicate intergradation with *nevadensis*. The specimens from Delano and Alila suggest intergradation with *xanthogenys*.

*Specimens examined*—Total number, 17, all from California, listed by counties from north to south, as follows: *Fresno County*: Coalinga, 1; 3 miles S Coalinga, 1. *Tulare County*: Alila (= Earlimart), 2. *Kern County*: Delano, 1; Buttonwillow, 9; Isabella, 1; Willow Spring, 1. *San Luis Obispo County*: 2 miles SW Simmler, 1.

*Mustela frenata inyoensis* new subspecies

*Type*—Male, adult, skull (with skeleton) and skin; No. 25907, Mus. Vert. Zool.; Carl Walter's Ranch, 2 miles N Independence, Inyo County, California; June 26, 1917; collected by A. C. Shelton; original No. 3143.

*Range*—From 3700 feet (Lone Pine) to at least 4000 feet (Alvord); Lower Sonoran Zone of floor of Owens Valley in Inyo County, California.

*Diagnosis*—Size: Medium (see measurements). Color: Large spot between eyes, band confluent with color of underparts, on each side of head extending anterodorsally anterior to each ear, upper throat, chin, lower lips and sometimes part or all of upper lips white; patch between eyes and bars in front of ears rarely tinged with some shade of yellowish; dark spot posterior to each angle of mouth present in four of five specimens examined; tip of tail black; remainder of upperparts, in summer, near (l) Brussels brown or tones 1 to 2 of raw umber of Oberthür and Dauthenay, pl. 301; slightly darker brown on forehead, nose and about eyes; in winter, near (j) snuff brown or lighter than Brussels brown with a smoked effect; underparts buff yellow, winter and summer; color of underparts extends distally on posterior sides of fore limbs over toes onto antipalmar faces of feet and wrists and on medial sides of hind limbs over antiplantar faces of toes; least width of color of underparts averaging, in 5 available specimens, 34 (24–42) per cent of greatest width of color of upperparts. Black tip of tail in two adult males, 45 and 60 mm. long; thus longer than hind foot and averaging 34 per cent of length of tail vertebrae. Skull and teeth: Male (type): See measurements. As described in *M. f. nigriauris* except for the following characters: Weight, 4.4 grams; basilar length, 44.7; postorbital breadth not less than width of basioccipital measured from medial margin of one foramen lacerum posterior to its opposite; length of tympanic bulla less than length of lower molar and premolar tooth-row. Female: adult unknown.

*Remarks*—*M. f. inyoensis*, as now known, is in general closely similar to *M. f. nevadensis* save for the presence of well-developed white facial markings like those found in weasels of the San Joaquin Valley and southern part of the coastal region of California.

*Specimens examined*—Total number, 5, all from Inyo County, California, by localities, from north to south, as follows: Alvord, 4000 feet, 1; Carl Walter's Ranch, 2 miles N Independence, 1; Lone Pine, 3.

*Mustela frenata texensis* new subspecies

*Type*—Male, adult, skull with skin of head, neck and tail; No. 14821, Amer. Mus. Nat. Hist.; Kerr County, Texas; September 17, 1897; collected by H. P. Attwater.

*Range*—Lower Sonoran Zone and possibly Upper Sonoran Zone of central Texas.



*Diagnosis*—Size: Largest of American weasels (subgenus *Mustela*), see measurements. Color: Spot between eyes, broad band, confluent with color of underparts, on each side of head extending anterodorsally anterior to each ear, and posterior two-thirds to half of each upper lip, white; remainder of sides and top of head, posteriorly to line connecting posterior margins of ears, blackish; dark spot posterior to each angle of mouth present or absent; tip of tail black; remainder of upperparts near Brussels brown; chin white; remainder of underparts near (16a) ochraceous buff (same color in juveniles and young), which color extends distally on posterior sides of fore limbs over fore feet and on medial sides of hind limbs to feet and sometimes onto upper sides of toes; least width of color of underparts near 47 per cent of greatest width of color of upperparts. Skull and teeth: Male: See measurements. As described in *M. f. nigriauris* except for following characters: Weight, 8.0 grams; basilar length 54.0; mastoid breadth less than postpalatal length; length of tympanic bulla more than length of lower molar and premolar tooth-row and usually longer than rostrum. Female: skull unknown.

*Remarks*—*M. f. texensis* closely resembles *M. f. frenata* except for much greater size.

*Specimens examined*—Total number, 4, from Texas, as follows: *Kerr County*, 2. *McLennan County*: 5 miles N Waco, 1; Erath, 1.

*Mustela frenata perotæ* new subspecies

*Type*—Female, adult, skull and skin; No. 54278, U. S. Nat. Mus., Biol. Surv. Coll.; 12500 feet, Cofre de Perote, Vera Cruz, Mexico; May 26, 1893; collected by E. W. Nelson; original No. 4864.

*Range*—From near 7500 feet (Perote) to 12500 feet, Cofre de Perote, Upper Sonoran and Transition (?) zones of mountains of eastern central Vera Cruz and Oaxaca.

*Diagnosis*—Size: Large (see measurements). Color: As described in *Mustela frenata texensis* except that: blackish of sides and top of head extends one-fourth of way back to shoulders from ears; throat and breast as well as chin white; remainder of underparts near (16'c) ochraceous buff; least width of color of underparts equals 36 per cent of greatest width of color of upperparts. Skull and teeth: Male: typical adult not seen. Female: See measurements. As described in *M. f. nigriauris* except for the following characters: Weight, 3.4 grams; basilar length, 43.5; zygomatic breadth less than distance between condylar foramen and M<sub>1</sub> or than between anterior palatine foramen and anterior margin of tympanic bulla; tympanic bulla as far posterior to foramen ovale as combined width of 5 or 6 upper incisors; height of tympanic bulla one-half to three-fifths distance from its anterior margin to foramen ovale; length of tympanic bulla more than length of lower molar and premolar tooth-row and longer than rostrum.

*Remarks*—Among named subspecies, *Mustela frenata frenata* is structurally more similar to *perotæ* which differs in farther posterior extension of the black markings of the head, restriction of color of underparts, much lower tympanic bulla, the height of which is less than, rather than more than, the distance from its anterior end to the foramen ovale.

Although the specimen from Cerro San Felipe, Oaxaca, is referred to *Mustela frenata perotæ*, the description of which it answers to best, that specimen in reality is an intergrade between several of the adjoining races. Thus, the range of typical *M. f. perotæ* is not known to include more than Cofre de Perote.

*Specimens examined*—Total number, 3, as follows: *Vera Cruz*: Cofre de Perote, 12500 feet, 1; *Perote*, 1. *Oaxaca*: Cerro San Felipe, 10000 feet, 1.





FIG. 6—Map showing geographic ranges of subspecies of two species *Mustela frenata* and *Mustela stolzmanni*.

- |                                |                             |                            |                                |
|--------------------------------|-----------------------------|----------------------------|--------------------------------|
| 1. <i>M. f. noveboracensis</i> | 12. <i>M. f. nevadensis</i> | 23. <i>M. f. inyoensis</i> | 34. <i>M. f. costaricensis</i> |
| 2. " <i>occisor</i>            | 13. " <i>effera</i>         | 24. " <i>neomexicana</i>   | 35. " <i>panamensis</i>        |
| 3. " <i>primulina</i>          | 14. " <i>washingtoni</i>    | 25. " <i>texensis</i>      | 36. " <i>meridana</i>          |
| 4. " <i>arthuri</i>            | 15. " <i>saturata</i>       | 26. " <i>frenata</i>       | 37. " <i>affinis</i>           |
| 5. " <i>olivacea</i>           | 16. " <i>altifrontalis</i>  | 27. " <i>leucoparia</i>    | 38. " <i>aureoventris</i>      |
| 6. " <i>peninsulae</i>         | 17. " <i>oregonensis</i>    | 28. " <i>perotæ</i>        | 39. " <i>helleri</i>           |
| 7. " <i>spadix</i>             | 18. " <i>munda</i>          | 29. " <i>macrophonus</i>   | 40. " <i>macrura</i>           |
| 8. " <i>longicauda</i>         | 19. " <i>xanthogenys</i>    | 30. " <i>goldmani</i>      | 41. " <i>agilis</i>            |
| 9. " <i>oribasa</i>            | 20. " <i>nigrauris</i>      | 31. " <i>tropicalis</i>    | 42. <i>M. s. stolzmanni</i>    |
| 10. " <i>alleni</i>            | 21. " <i>latirostra</i>     | 32. " <i>perda</i>         | 43. <i>M. s. paracensis</i>    |
| 11. " <i>arizonensis</i>       | 22. " <i>pulchra</i>        | 33. " <i>nicaraguæ</i>     |                                |



	M.V.Z.	♀ ad.	Hayward, Cal.	40.7	15.3	11.8	8.8	13.9	21.8	24.9	14.2	7.9	3.0	12.4	11.5
5851	M.V.Z.	♀ ad.	Palo Alto, Cal.	41.2	16.2	11.1	8.6	14.3	21.7	24.8	13.4	7.8	3.0	12.6	11.0
30372	M.V.Z.	♀ ad.	Berkeley, Cal.	38											
38347	M.V.Z.	♀ ad.	Berkeley, Cal.	37											
19120	M.V.Z.														
<i>Mustela frenata latirostra</i>															
3257	M.V.Z.	♂ ad.	San Diego, Cal.	42	44.4	17.8	10.2	15.0	23.5	27.6	15.6	8.4	3.9	14.0	12.8
52701	U.S.N.M.	♂ ad.	El Vido, Cal.		43.7	16.9	9.9	14.3	24.0		14.7	8.7	4.0	14.2	13.4
52702	U.S.N.M.	♂ ad.	El Cajon, Cal.		43.2	16.7	13.9	10.0	24.0	27.2	15.1	8.2	4.2	14.0	12.5
3258	M.V.Z.	♂ ad.	San Diego, Cal.	40	42.5	16.6	14.1	12.1	14.7	24.0	13.1	8.1	3.9	14.3	13.5
20	Stephens <sup>e</sup>	♂ ad.	San Jacinto Plain, Cal.		41.9	16.9	13.1	10.6	14.0	28.2	14.7	8.0	3.2	14.0	12.0
22	Stephens	♀ ad.	Santa Ysabel, Cal.		43.1	17.0	13.4	10.6	14.6	23.9	15.0	8.3	3.8	14.1	13.0
19	Stephens	♀ ad.	Ballena, Cal.	39	40.1	15.5	11.7	9.3	13.1	21.9	14.2	8.0	3.0	14.0	11.3
7194	San Diego <sup>d</sup>	♀ ad.	Jamaca, Cal.	35	39.8	15.0	12.3	9.3	13.5	21.6	13.7	8.1	3.2	12.0	11.2
							9.1	13.7	20.2	23.7	13.7	7.0	2.9	12.6	11.5
<i>Mustela frenata pulchra</i>															
335	C.A.S. <sup>e</sup>	♂ ad.		51	48.6	18.8	15.2	11.6	17.2	27.4	16.7	9.1	3.6	16.2	13.7
337	C.A.S.	♂ ad.		55	48.6	18.8	15.0	11.8	17.2	27.1	16.6	9.0	3.5	16.5	14.3
16668	M.V.Z.	♂ ad.	Buttontwillow, Cal.	49	48.1	18.8	14.8	12.0	17.1	31.2	16.4	9.2	3.6	15.2	14.0
137935	U.S.N.M.	♂ ad.		47	47.2	18.2	14.0	10.3	16.0	26.1	15.6	8.5	3.3	15.0	12.9
336	C.A.S.	♂ ad.		51	47.0	18.3	14.5	11.5	16.5	27.0	15.5	9.1	3.2	15.0	13.0
338	C.A.S.	♂ ad.		47	46.0	17.4	14.7	11.3	16.1	26.3	15.9	8.9	3.7	15.0	13.3
				50	47.6	18.4	14.7	11.4	16.7	26.9	16.1	9.0	3.5	15.5	13.5
<i>Mustela frenata ingoensis</i>															
25907	M.V.Z.	♂ ad.	Type Locality	42	44.7	17.3	13.3	10.8	15.9	25.3	15.9	9.0	3.7	15.0	13.2
25392	U.S.N.M.	♂ ad.	Lone Pine, Cal.	44	43.0	16.0	12.5	9.7	15.0	23.1	14.6	8.1	3.2	13.7	11.8
32805															
<i>Mustela frenata texensis</i>															
14821	A.M.N.H.	♂ ad.	Kerr Co., Tex.		54.0	19.2	16.0	12.6	28.6	35.1	17.5	8.0	3.5	16.7	15.1
15476	M.C.Z.	♂ yg.	Kerr Co., Tex.		53.3	18.9	16.3	12.8	28.2	34.8	18.0	8.3	4.0	16.0	15.0
2017	Baylor	♂ sad.	5 mi. N. Waco, Tex.		52.0	18.3	16.5	13.5	29.2		18.0	9.1		16.3	15.6
<i>Mustela frenata perotae</i>															
54278	U.S.N.M.	♀ ad.	Perote, Mex.	45	43.5	15.5	12.3	10.3	23.2	25.5	15.0	7.0	2.0	12.0	13.7

\* From posterior margin of postorbital process of frontal to superior border of anterior nares.

<sup>a</sup> Private coll., S. J. Jewett.<sup>b</sup> Leland Stanford Jr. Univ.<sup>c</sup> Private coll., Frank Stephens.<sup>d</sup> San Diego Soc. Nat. Hist.<sup>e</sup> Calif. Acad. Sci.



## REVISED CLASSIFICATION OF LONG-TAILED WEASELS

The following list of American long-tailed weasels comprises, in so far as known to the writer, all the named subspecies which are recognizable on the basis of distinctive structural features. Names (synonyms) which have been proposed for American long-tailed weasels, now deemed indistinguishable from previously named kinds, are to be found in italicized type immediately below the citation to the accepted name.

In this group of animals, which is continuously distributed over the mainland of a large part of the Americas, intergradation or lack of it is accepted as the criterion of subspecies and species, respectively. That is to say, if at a place where ranges of two kinds meet, the populations freely interbreed in a state of nature, the two kinds are said to intergrade and accordingly are treated as subspecies of one species. If, on the other hand, the two kinds do not cross-breed at any place where their ranges meet or overlap, this constitutes lack of intergradation, and the two kinds, therefore, are treated as distinct species.

1. *Mustela frenata noveboracensis* (Emmons).

1840. *Putorius noveboracensis* Emmons, Rep. Quadr. Massachusetts, p. 45.

1854. *Putorius agilis* Audubon and Bachman, The Quadrapeds of North America, New York, p. 184. Type a female from northern New York; not *Mustela agilis* Tschudi, 1844.

1899. *Putorius noveboracensis notius* Bangs, Proc. New England Zool. Club, vol. 1, p. 53. June 9, 1899. Type from Weaverville, Buncombe County, North Carolina.

*Type Locality*—State of Massachusetts.

*Range*—Altitudinally, sea-level to highest parts of mountains of eastern United States; Canadian Zone of Ontario and Quebec southward through eastern United States in Canadian, Transition and Upper Austral zones to and including upper edge of Lower Austral Zone in the Carolinas and northern parts of Georgia, Alabama and Mississippi; westward from the Atlantic Coast to the St. Croix and Mississippi rivers.

2. *Mustela frenata occisor* (Bangs).

1899. *Putorius occisor* Bangs, Proc. New England Zool. Club, vol. 1, p. 54. June 9, 1899.

*Type Locality*—Bucksport, Hancock County, Maine.

*Range*—Canadian Zone and possibly Transition Zone of Maine.

3. *Mustela frenata primulina* Jackson.

1913. *Mustela primulina* Jackson, Proc. Biol. Soc. Washington, vol. 26, p. 123. May 21, 1913.

*Type Locality*—Five miles northeast of Avilla, Jasper County, Missouri.

*Range*—Upper and Lower Austral zones west of the Mississippi River in Missouri, the southeastern half of Iowa, eastern halves of Kansas and Oklahoma and northern part of Arkansas. Southern and southwestern limits of range undetermined.

3A. *Mustela frenata gracilis* (Brown).

1908. *Putorius gracilis* Brown, Mem. Amer. Mus. Nat. Hist., vol. 9, pt. 4, p. 182, pl. 17. 1908.

*Type Locality*—Conard Fissure, Pleistocene deposit, 4 miles west of Willcockson and 15 miles south of Harrison, near the northern line of Newton County, Arkansas.

*Range*—Known only from the type locality, a Pleistocene fossil deposit.

4. *Mustela frenata arthuri* Hall.

1927. *Mustela noveboracensis arthuri* Hall, Proc. Biol. Soc. Washington, vol. 40, p. 193. December 2, 1927.

*Type Locality*—Remy, St. James Parish, Louisiana.

*Range*—Known certainly only from the eastern half of southern Louisiana in the Lower Austral Zone.

5. *Mustela frenata olivacea* Howell.

1913. *Mustela peninsulæ olivacea* Howell, Proc. Biol. Soc. Washington, vol. 26, p. 139. May 21, 1913.

*Type Locality*—Autaugaville, Autauga County, Alabama.

*Range*—Lower and Upper Austral zones in eastern Mississippi, Alabama, Georgia, South Carolina and northern Florida.

6. *Mustela frenata peninsulæ* (Rhoads).

1894. *Putorius peninsulæ* Rhoads, Proc. Acad. Nat. Sci., Philadelphia, p. 152. June 19, 1894.

*Type Locality*—Hudson's, Pasco County [14 miles north of Tarpon Springs], Florida.

*Range*—Austral and probably Tropical zones of Florida south of 29° N latitude.

7. *Mustela frenata spadix* (Bangs).

1896. *Putorius longicauda spadix* Bangs, Proc. Biol. Soc. Washington, vol. 10, p. 8. February 25, 1896.

*Type Locality*—Fort Snelling, Hennepin County, Minnesota.

*Range*—Upper Austral and Transition zones of Minnesota, northern and western Iowa, southeastern North Dakota, eastern part of South Dakota and northeastern Nebraska.

8. *Mustela frenata longicauda* Bonaparte.

1838. *Mustela longicauda* Bonaparte, Charlesworth's Mag. Nat. Hist., vol. 2, p. 38. January, 1838.

1877. *Putorius culbertsoni* Coues, Fur-bearing animals . . . , p. 136. (*Nomen nudum*).

*Type Locality*—Carlton House, on north Saskatchewan River, Saskatchewan.

*Range*—Transition and Sonoran zones of the Great Plains, southward from central Alberta, Saskatchewan and southern Manitoba through eastern Montana, the Dakotas and Nebraska into southeastern Wyoming, northeastern Colorado and western Kansas.

9. *Mustela frenata oribasa* (Bangs).

1899. *Putorius (Arctogale) longicauda oribasus* Bangs, Proc. New England Zool. Club, vol. 1, p. 81. December 27, 1899.

*Type Locality*—Source of Kettle River, 7500 feet, British Columbia.

*Range*—Canadian and Hudsonian zones from near lat. 53° N in British Columbia along the Fraser River south to Lillooet, in the Caribou and Monashee Mountains, probably in the Selkirks and Rockies, and through the Rockies of Montana into extreme northern Wyoming.

10. *Mustela frenata alleni* (Merriam).

1896. *Putorius alleni* Merriam, North Amer. Fauna, No. 11, p. 24. June 30, 1896.

*Type Locality*—Custer, Black Hills, Custer County, South Dakota.

*Range*—Canadian, Transition, and Upper Sonoran zones of the Black Hills of South Dakota and adjacent semi-bad-land territory of Wyoming and Nebraska southward to Scottsbluff.

11. *Mustela frenata arizonensis* Mearns.

1891. *Putorius arizonensis* Mearns, Bull. Amer. Mus. Nat. Hist., vol. 3, p. 234. June 5, 1891.

*Type Locality*—San Francisco Forest [then, 1886?], Yavapai County, Arizona.

*Range*—Transition to Hudsonian zones of Arizona and extreme western New Mexico, along the Colorado River and south of the Little Colorado River, from San Francisco Mountain region along Mogollon Plateau to extreme western New Mexico.

12. *Mustela frenata nevadensis* Hall.

Present paper, p. 91.

*Type Locality*—Three miles east of Baker, White Pine County, Nevada.

*Range*—Altitudinally, 700 feet (at Wenatchee, Washington) to the highest parts of mountains of western United States; Upper Sonoran Zone to Arctic-Alpine Zone; southern British Columbia in the Cascades and territory west to Monashee Mountains, and Nelson, southward in the Cascades of northern Washington, over western Washington, Idaho, Utah and Nevada to north-eastern Arizona and northern New Mexico; westward from the eastern base of the Rocky Mountains in Colorado to the western base of the Sierra Nevada and Cascades of California and to the Cascades of southern Oregon.

13. *Mustela frenata effera* Hall.

Present paper, p. 93.

*Type Locality*—Ironsides, 4000 feet, Malheur County, Oregon.

*Range*—Upper Sonoran to Arctic-Alpine zones of northern two-thirds of Oregon east of the Cascades and southeastern Washington south of the Snake River.

14. *Mustela frenata washingtoni* Merriam.

1896. *Putorius washingtoni* Merriam, North Amer. Fauna, No. 11, p. 18. June 30, 1896.

*Type Locality*—Trout Lake, base of Mount Adams, Washington.

*Range*—Altitudinally, from near 2000 feet at Trout Lake up to the highest parts of the Cascade Range from Mount Jefferson, Oregon, north to Mount Rainier, Washington; Upper Sonoran Zone to Arctic-Alpine Zone.

15. *Mustela frenata saturata* (Merriam).

1896. *Putorius saturatus* Merriam, North Amer. Fauna, No. 11, p. 21. June 30, 1896.

*Type Locality*—Siskiyou, Jackson County, Oregon.

*Range*—Transition and Boreal zones of Siskiyou and Trinity mountains in southern Oregon and northwestern California.



16. *Mustela frenata altifrontalis* Hall.

Present paper, p. 94.

*Type Locality*—Tillamook, Tillamook County, Oregon.

*Range*—Altitudinally, from sea-level up to at least 4800 feet (Mount Baker) in the Transition Zone of the humid coastal region of Oregon, Washington, and extreme southwestern British Columbia.

17. *Mustela frenata oregonensis* (Merriam).

1896. *Putorius xanthogenys oregonensis* Merriam, North Amer. Fauna, No. 11, p. 25. June 30, 1896.

*Type Locality*—Grants Pass, Rogue River Valley, Josephine County, Oregon.

*Range*—Transition and Canadian zones along coast of northern California and southern Oregon from Humboldt County, California, north through Curry County, Oregon, thence inland, west of the Cascades, north to the Columbia River.

18. *Mustela frenata munda* (Bangs).

1899. *Putorius xanthogenys mundus* Bangs, Proc. New England Zool. Club, vol. 1, p. 56. June 9, 1899.

*Type Locality*—Point Reyes, Marin County, California.

*Range*—Sea-level to at least 6000 feet (South Yolla Bolly Mountain, Trinity County); Upper Sonoran and Transition zones of the coast and Coast Range of northwestern California from the Golden Gate northward into southern Humboldt and Trinity counties.

19. *Mustela frenata xanthogenys* Gray.

1843. *Mustela xanthogenys* Gray, Ann. and Mag. Nat. Hist., vol. 11, p. 118. February, 1843.

*Type Locality*—Probably Sacramento River, below junction with Feather River, California.

*Range*—Altitudinally, under 600 feet; Lower Sonoran and Upper Sonoran zones of probably the Sacramento Valley and all but the southern end of the San Joaquin Valley, California.

20. *Mustela frenata nigriauris* Hall.

Present paper, p. 95.

*Type Locality*—2½ miles E Santa Cruz, Santa Cruz County, California.

*Range*—Altitudinally, sea-level to highest parts of the Coast Range in the Sonoran and Transition zones of Coast Range and coast of California from San Francisco Bay south to Point Conception, Santa Barbara County, California.

21. *Mustela frenata latirostra* Hall.

Present paper, p. 96.

*Type Locality*—San Diego, San Diego County, California.

*Range*—Sea-level to 8000 feet (Tahquitz Valley, San Jacinto Mountains) in Sonoran and Transition zones of coast and mountains west of Mojave and Imperial deserts of southern California, from Point Conception and Cuyama Valley, southward to Mexican boundary.

22. *Mustela frenata pulchra* Hall.

Present paper, p. 98.

*Type Locality*—Buttonwillow, Kern County, California.

*Range*—Altitudinally, 300 feet to 2500 feet in Upper and Lower Sonoran zones of southern end of San Joaquin Valley, and mountains at southern end of Valley, California.

23. *Mustela frenata inyoensis* Hall.

Present paper, p. 99.

*Type Locality*—Carl Walter's Ranch, 2 miles north of Independence, Inyo County, California.

*Range*—From 3700 feet (Lone Pine) to at least 4000 feet (Alvord) in Lower Sonoran Zone on floor of Owens Valley, Inyo County, California.

24. *Mustela frenata neomexicana* (Barber and Cockerell).

1898. *Putorius frenatus neomexicanus* Barber and Cockerell, Proc. Acad. Nat. Sci. Philadelphia, p. 188. May 3, 1898.

*Type Locality*—Armstrongs Lake, Mesilla Valley, Dona Ana County, New Mexico.

*Range*—Altitudinally, 3800 feet (type locality) to 8000 feet (Chiricahua Mountains) in Upper and Lower Sonoran zones of northern Mexico, southeastern Arizona, New Mexico, western Texas and north to southwestern Kansas.

25. *Mustela frenata texensis* Hall.

Present paper, p. 99.

*Type Locality*—Kerr County, Texas.

*Range*—Lower and possibly Upper Sonoran zones of central Texas.

26. *Mustela frenata frenata* Lichtenstein.

1832 (1831?). *Mustela frenata* Lichtenstein, Darstellung neuer oder wenig bekannter Säugethiere, pl. 42 and corresponding text, unpagged.

1813. *Mustela brasiliensis* Sevestianoff (not of Gmelin, 1778), Mem. Acad. Imp. Sci. St. Petersburg, vol. 4, pp. 356-363 of description and pl. 4 with name.

*Type Locality*—Valley of Mexico, near Mexico City.

*Range*—Altitudinally, sea-level (Brownsville, Texas) to 7600 feet (Tlalpam, Mexico); Sonoran Zone of southern Texas and Mexico as far south as Mexico City.

27. *Mustela frenata leucoparia* (Merriam).

1896. *Putorius frenatus leucoparia* Merriam, North Amer. Fauna, No. 11, p. 29. June 30, 1896.

*Type Locality*—Patzcuaro, Michoacan, Mexico.

*Range*—Sonoran and Transition (?) zones of mountains west of Mexico City in Michoacan and Narayit.

28. *Mustela frenata perotæ* Hall.

Present paper, p. 100.

*Type Locality*—Elevation of 12,500 feet, Cofre de Perote, Vera Cruz, Mexico.

*Range*—From near 7500 feet (Perote) to 12,500 feet, Cofre de Perote, Upper Sonoran and Transition (?) zones of mountains of eastern central Vera Cruz and Oaxaca.

29. *Mustela frenata macrophonus* (Elliot).

1905. *Putorius macrophonus* Elliot, Proc. Biol. Soc. Washington, vol. 18, p. 235. December 9, 1905.

*Type Locality*—Achotál, Vera Cruz, Mexico.

*Range*—Upper Tropical Zone (?) of mountains along eastern border of southern Vera Cruz, Mexico.

30. *Mustela frenata goldmani* (Merriam).

1896. *Putorius frenatus goldmani* Merriam, North Amer. Fauna, No. 11, p. 28. June 30, 1896.

*Type Locality*—Pinabete, Chiapas, Mexico.

*Range*—Altitudinally, 2500 feet (El Cipres, Guatemala) to 9500 feet (near Tecpam, Guatemala); Upper Tropical zones of mountains and western coasts of southern Mexico, Guatemala, and Salvador.

31. *Mustela frenata tropicalis* (Merriam).

1896. *Putorius tropicalis* Merriam, North Amer. Fauna, No. 11, p. 30. June 30, 1896.

*Type Locality*—Jico, Vera Cruz, Mexico.

*Range*—Altitudinally, as now known, 4000 feet to 5000 feet in Tropical Zone of Vera Cruz, Mexico.

32. *Mustela frenata perda* (Merriam).

1902. *Putorius tropicalis perdus* Merriam, Proc. Biol. Soc. Washington, vol. 15, p. 67. March 22, 1902.

*Type Locality*—Teapa, Tabasco, Mexico.

*Range*—Altitudinally, 1000 feet (Catemaco) to 4000 feet (San Vicente) in Lower Tropical Zone south from southern Vera Cruz through southern Mexico into Guatemala.

33. *Mustela frenata nicaraguæ* Allen.

1916. *Mustela tropicalis nicaraguæ* Allen, Bull. Amer. Mus. Nat. Hist., vol. 35, p. 100. April 28, 1916.

*Type Locality*—Matagalpa, Nicaragua.

*Range*—Nicaragua.

34. *Mustela frenata costaricensis* Goldman.

1912. *Mustela costaricensis* Goldman, Proc. Biol. Soc. Washington, vol. 25, p. 9. January 23, 1912.

*Type Locality*—San José, Costa Rica.

*Range*—Costa Rica.

35. *Mustela frenata panamensis* Hall.

1932. *Mustela frenata panamensis* Hall, Proc. Biol. Soc. Washington, vol. 45, p. 139. September 9, 1932.

*Type Locality*—Rio Indio, Canal Zone, near Gatun, Panama.



*Range*—Sea-level (type locality) to 5800 feet (Boquete); Upper and Lower Tropical zones of Panama.

36. *Mustela frenata meridana* Hollister.

1914. *Mustela meridana* Hollister, Proc. Biol. Soc. Washington, vol. 27, p. 143. July 10, 1914.

*Type Locality*—Montes de Merida, 5350 feet, near Merida, Venezuela.

*Range*—Near sea-level (San Julian) to 8500 feet (Montes de Culata, Merida, Venezuela), and 9000 feet (Santa Elena, Colombia); Temperate to Subtropical zones of Venezuela and northern and western Colombia.

37. *Mustela frenata affinis* Gray.

1874. *Mustela affinis* Gray, Ann. and Mag. Nat. Hist., vol. 14 (ser. 4), p. 375.

*Type Locality*—New Granada [=Colombia]. Type locality restricted by Allen (Bull. Amer. Mus. Nat. Hist., vol. 35, p. 99. 1916) to Bogota, Colombia.

*Range*—Altitudinally, 4600 feet (Quetame) to 9154 feet (El Carmen), Tropical Zone to Temperate Zone of eastern Andes of Colombia.

38. *Mustela frenata aureoventris* Gray.

1864. *Mustela aureoventris* Gray, Proc. Zool. Soc. London, for 1864, p. 55, pl. 8. February 9, 1864.

1877. *Putorius (Gale) brasiliensis* var. *æquatorialis* Coues, Fur-bearing animals . . . , p. 142. Proposed "merely as a substitute for Gray's [supposedly] preoccupied name," *aureoventris*.

*Type Locality*—Type specimen received from Quito but probably taken at a lower altitude in Ecuador or Peru.

*Range*—Known with certainty only from the Subtropical Zone of Peru.

39. *Mustela frenata helleri* Hall.

1935. *Mustela frenata helleri* Hall, Proc. Biol. Soc. Washington, vol. 48, p. 143, August 22, 1935.

*Type Locality*—Hacienda San Antonio, 3000 feet, Rio Chinchao, Peru.

*Range*—Altitudinally, 3000 feet (type locality) to 6700 feet (Ambo), Tropical and Subtropical zones of eastern Peru.

40. *Mustela frenata macrura* Taczanowski.

1874. *Mustela macrura* Taczanowski, Proc. Zool. Soc. London, for 1874, p. 311, pl. 48. May 19, 1874.

1881. *Mustela jelskii* Taczanowski, Proc. Zool. Soc. London, for 1881, p. 647. May 17, 1881. Type specimen from Cutervo, Peru.

*Type Locality*—Lake Junin, central Peru.

*Range*—Altitudinally, 8000 feet to at least 11000 feet (Nára Papallacta); Upper Subtropical and Temperate zones of central Peru and Ecuador north from Lake Titicaca to San Antonio, northern Ecuador.

41. *Mustela frenata agilis* Tschudi.

1844. *Mustela agilis* Tschudi, Untersuchungen uber die Fauna Peruana, Therologie, St. Gallen, p. 110.

*Type Locality*—Cold, barren highlands of the Cordillera of Peru.

*Range*—High, barren Cordillera of Peru (see Tschudi, orig. descr.); as here restricted, Temperate Zone of western Andes and intermountain valleys of Peru.

42. *Mustela stolzmanni stolzmanni* Taczanowski.

1881. *Mustela stolzmanni* Taczanowski, Proc. Zool. Soc. London, for 1881, p. 835. November 15, 1881.

*Type Locality*—Yurimaguas, Peru.

*Range*—Known only from the type locality which is in the Tropical Zone.

43. *Mustela stolzmanni paraensis* Goeldi.

1897. *Putorius (Mustela) braziliensis paraensis* Goeldi, Zool. Jahrb., abt. f. systematik, geogr. u. biol., vol. 10, p. 560, pl. 21. September 15, 1897.

*Type Locality*—Near Pará, Ward of Marco de Legoa, Brazil.

*Range*—Known only from the type locality which is in the Tropical Zone.

*Mustela cicognanii angustidens* (Brown)

*Putorius cicognanii angustidens* Brown (1908, p. 181, pl. 17).

*Mustela cicognanii angustidens*, Hay (1914, p. 32; 1924, p. 252; 1930, p. 528).

*Type*—Female?, adult, skull and lower jaws lacking zygomata, right P2 and incisors, No. 12432, Amer. Mus. Nat. Hist.; from Conard Fissure, four miles west of Willcockson, Newton County, Arkansas, collected at some time during the period 1903 to 1905 inclusive.

*Remarks*—According to Brown (1908, p. 181) this subspecies most nearly resembles *P. cicognanii* (origin of specimens not stated) but differs from that form as follows:

"The skulls average slightly smaller; upper molar narrower anteroposteriorly, and the postorbital constriction and process are well marked.

"The female skulls are small, narrow and as in *P. cicognanii*, with, however, a marked postorbital constriction and a well developed postorbital process. The zygomata is bowed outward slightly in skull No. 12435, the only specimen in which it is complete. The brain-case is elongated and flattened vertically and not as cylindrical as in *P. cicognanii*. The auditory bullæ are small, narrow and subcylindrical, but shorter by one millimeter than in *P. cicognanii* of the same size. The bullæ are almost continuous anteriorly, but not inflated as much posteriorly as in the recent species, a feature which gives the skull less vertical depth at this point.

"The postglenoid surface is extensive, as in *P. cicognanii*, but the space separating the pterygoids is much narrower.

"There is a marked reduction in p<sup>2</sup>, which is much smaller than in *P. cicognanii*."

The characters separating the subspecies of *P. cicognanii* in many cases are not readily apparent. Furthermore, in his study of the American weasels, now under way, the present writer has not, by first hand examination satisfied himself as to the nature of the differences separating the subspecies of *Mustela cicognanii*. Thus the present account is taken directly from Brown (*op. cit.*).

*Mustela frenata noveboracensis* (Emmons)

*Putorius ermineus*, Leidy (1880, p. 348); Leidy (1889, p. 5 not seen).

*Putorius noveboracensis*, Rhoads (1903, p. 229).

*Mustela noveboracensis*, Hay (1923, p. 310; 1930, p. 529).

*Remarks*—The remains referred to in the literature above cited all are those taken from Hartmans Cave, three and one-half miles southwest of Stroudsburg, Pennsylvania. None of the specimens has been examined by me and I have no way of knowing whether they are of Recent or of Pleistocene age.



*Mustela frenata nevadensis* Hall

*Putorius arizonensis*, Sinclair (1903, p. 711; 1904, p. 17); Furlong (1904, p. 54; 1906, p. 243); Miller, L. H. (1912, p. 70).

*Mustela arizonensis*, Stock (1918, pp. 468-469); Merriam and Stock (1925, p. 10); Stock (1925, p. 113); Hay (1927, p. 214; 1930, p. 528).

*Remarks*—The literature cited above all pertains to remains from Potter Creek and Samwel caves, Shasta County, California. Material examined, all in the collection of vertebrate fossils at the University of California, Berkeley, is as follows: From Potter Creek Cave: No. 6078, left lower jaw of male; No. 8528, right lower jaw of male (not same individual as No. 6078); and No. 4412, right lower jaw of a female. From Samwel Cave: No. 9655, anterior three-fourths of cranium of male; No. 9002, left lower jaw of female; and two uncatalogued lower jaws, one the right mandible of a juvenile and the other part of the left mandible of an adult. These specimens agree with Recent *Mustela frenata nevadensis* from the same section of California. The association with such extinct forms as *Preptoceras* and ground sloths argues for Pleistocene age of the remains but of course, the weasels may have entered at a later time than did the *Preptoceras* and ground sloths.

*Mustela frenata gracilis* (Brown)

*Putorius gracilis* Brown (1908, p. 182, pl. 17).

*Mustela gracilis*, Hay (1914, p. 32; 1924, p. 252; 1930, p. 528).

*Type*—Skull, adult, assumedly of female, lacking lower jaws, zygomata, right canine and incisors; No. 12431, collection of vertebrate fossils, American Museum of Natural History; from Conard Fissure, four miles west of Willcockson, Newton County, Arkansas, collected some time during the period 1903 to 1905 inclusive.

*Remarks*—The type specimen was the only individual referred by Brown (1908) to this species. The remaining material of weasels from this deposit was referred by Brown to a second new form, *Putorius cicognanii angustidens*. Examination of the original materials convinces the writer, too, that the remains, save that of No. 12431, are of the species *cicognanii*. No. 12431 itself may possibly be *cicognanii* but is far more probably of the species *frenata*. The uncertainty is due to the fact that an occasional skull alone of a subadult male *cicognanii* is extremely difficult certainly to distinguish from a skull alone of an adult female *frenata*. This is true among Recent specimens in the northern Mississippi Valley today; more exactly in Iowa and southern Minnesota when the females of *frenata*, oftentimes intergrades between the subspecies *Mustela frenata longicauda*, *M. f. noveboracensis* and *M. f. primulina*, by the skull alone are next to indistinguishable from certain unusually slender skulls of male *cicognanii*. At other places where the ranges of the two species meet, this difficulty is not so often encountered.

The type specimen of *gracilis* surely is an adult and because of its small size is thought to be a female. Of known long-tailed weasels of the species *frenata*, *gracilis* is structurally nearest to *M. f. primulina* which occurs in the same region today and to *M. f. noveboracensis*, the long-tailed weasel of the eastern United States. *M. gracilis* differs from *noveboracensis* and agrees with *primulina* in possessing well-marked temporal ridges which fuse to form a low sagittal crest, in having the mastoid processes projecting farther, laterally beyond the braincase, in having the anterior ends of the tympanic bullæ produced below the squamosal rather than on same plane with squamosal, and in having the bullæ more inflated anteromedially. *M. gracilis* differs from both *noveboracensis* (97 ♂ and 56 ♀ skulls of comparable age) and *primulina* (64 ♂ and 24 ♀ skulls of comparable age) in



that the zygomatic breadth amounts to less than 58 per cent of the basilar length. Another difference from any one of the female skulls of *primulina* is the longer rostrum, which, measured from the posterior base of the post-orbital process of the frontal to the anterior end of the nasal on the same side, amounts to more than 35 per cent of the basilar length. As pointed out by Brown (1908, p. 182) this specimen represents the extreme of slender skull among weasels.

Selected measurements of No. 12431, the type specimen of *Mustela gracilis*, are as follows: Basilar length of Hensel, 38.1 mm.; length of upper tooth rows, 14.3 to 14.4; breadth of rostrum, 11.0; interorbital breadth, 8.5; orbitonasal length, 13.6; mastoid breadth, 18.2; length of tympanic bulla, 13.0; breadth of tympanic bulla, 6.3; depth of tympanic bulla, 3.25; outside length of P<sub>4</sub>, 4.5; inside length of P<sub>4</sub>, 4.7; breadth of M<sub>1</sub>, 3.4; length of inner moiety of M<sub>1</sub>, 1.8; depth of skull at anterior margin of basioccipital, 12.2; depth of skull at posterior borders of last upper molars, 11.3.

#### *Mustela frenata nigriauris* Hall

*Remarks*—The collection of vertebrate fossils at the California Institute of Technology contains a nearly complete skull, and lower jaw possibly of the same individual, from one of the excavations (C. I. T. loc. No. 138) made in the asphalt deposits at McKittrick, Kern County, California. The subspecies of *Mustela frenata* found in the region of McKittrick today (see page 99 for known localities of occurrence and map on page 101) is *Mustela frenata pulchra*. Its skull, as set forth on page 98, differs from that of the two coastal subspecies, *M. f. nigriauris* and *M. f. latirostra* in a way which permits satisfactory subspecific identification of the skulls alone.

The skull from McKittrick, allowing for differences due to its lesser age, is a duplicate of the skull of a Recent adult male, No. 46723, Mus. Vert. Zool., of the coastal subspecies, from 5 miles southeast of Santa Margarita, San Luis Obispo County. This Recent skull, others from places in the coastal district to the southwest of McKittrick, and the fossil one from McKittrick, are intermediate in structural features between *M. f. latirostra* to the south and *M. f. nigriauris* to the north, though decidedly nearer the latter.

The skull from McKittrick, then, is of the subspecies *nigriauris* which does not occur in that region today but instead farther to the westward in the more humid coastal area.

#### *Mustela frenata latirostra* Hall

*Putorius* sp., Miller, L. H. (1912, p. 79).

*Mustela* sp., Stock (1925, p. 30); Hay (1927, p. 184); Hay (1930, p. 529, part).

*Mustela*, Wilson (1933, p. 66).

"*Mustela*, a species of the living marten," Osborn (1925, p. 531).

*Martes*, Stock (1929, p. 285).

"Weasel (*Mustela*)," Stock (1930B, p. 38).

*Remarks*—The writer has examined fifty-three skulls of weasels from Rancho La Brea. It is to this material that the above references apply. The fossil specimens examined are in the Los Angeles Museum of History, Science and Art and in the University of California Museum of Palæontology at Berkeley. With two exceptions the specimens clearly are referable to (not merely indistinguishable from) the subspecies inhabiting the same region today.

The two exceptions are specimens bearing numbers as follows:  $\frac{16}{20-27}$  and  $\frac{16}{20-27}$ . The latter is not fully adult. Among North American weasels (excluding minks and the black-footed ferret) it seems to be exceeded in size only by *Mustela frenata texensis*. At first it was thought that this skull might represent some one of the larger subspecies, as for example *Mustela frenata neomexicana* next adjacent on the east. However, the mastoid process is shaped as in *latirostra* and not as in *neomexicana*. No.  $\frac{16}{20-27}$  also is larger than *latirostra* or than individuals of any of the subspecies along the coast of California. This specimen is adult and displays characters which show it to be of the same stock as the Recent bridled weasels of California and not of the *neomexicana* type. These two specimens are considered to be "giants" of the Rancho La Brea population which otherwise appears to be the same as the Recent population living in the vicinity of Los Angeles, California. Even though nearly one hundred Recent specimens of *latirostra* have been examined, no specimen as large as either of these two La Brea individuals has been noted.

The skull from the asphalt deposit at Carpinteria recorded by Wilson (1933, p. 66) is indistinguishable from selected specimens from Rancho La Brea and Recent specimens from Los Angeles County. With these other specimens the one from Carpinteria is referred to *M. f. latirostra*, the race to which it is thought Recent weasels from Carpinteria would be referred.

*Mustela vison* cf *mink* (Peale and Beauvois)

*Putorius vison*, Allen (1876, p. 333); Hay (1902, p. 768).

*Mustela vison*, Hay (1930, p. 529, part).

*Mustela* cf *vison*, Gidley (1913, p. 96).

*Mustela vison*?, Hay (1923, p. 350).

*mink*, Gidley (1920, p. 283).

*Remarks*—The citations to literature given above under the first two names have to do with remains from caves in Pennsylvania first recorded by Allen (1876, p. 333). The present writer has not seen the material and does not know whether even Allen thought it was of Pleistocene age.

The remaining citations given above pertain to specimens from the Cumberland Cave deposit, 4 miles northwest of Cumberland, Maryland. Of these Dr. Gazin has kindly sent to me for examination from the collection of the United States National Museum, eight specimens. Four of these, each showing the upper dentition, and comprising more or less of the skull, bear catalogue numbers 8156, 11880, 12005 and 12354. The other four, numbers 8212, 11879, 12004 and 12047, are lower jaws with teeth.

Of Recent specimens of *Mustela vison mink* I have had available for comparison only one series of skulls; 13 males and 7 females from Talbot County, Georgia. In comparing the fossils with these no differences, judged to be of systematic worth, were found in the relative size of parts of the skull or teeth. Furthermore, most of the linear measurements of skull and teeth, in the fossil population is exceeded in both directions by the series of Recent animals. The few measurements of the fossils which do fall outside the range shown by the Recent specimens are less than in the Recent series. However, it is thought that farther north than Talbot County, Georgia, the living mink averages smaller. Hollister (1913) points out that *Mustela vison vison*, which occurs just to the north of Maryland, is the smallest form and indicates that an increase in size occurs to the southward in *M. f. mink*,



and in *M. f. lutensis*, of still more southern distribution, the largest of the three. One would infer that specimens from the northern part of the range of *M. f. mink* would be smaller than those from as far south as Talbot County, Georgia—some probably as small as the smallest of the fossil specimens. In any event, Recent specimens of the species *Mustela vison* are as small as the smallest of these fossils, for among 270 skulls of *M. v. energumenos* and *M. v. æstuarina* in the Museum of Vertebrate Zoology there are female specimens with teeth as small as, and in most measurements smaller than, those of the smallest fossil specimens.

In summary, no difference in size, or in any other feature, is found to distinguish fossil specimens of the Cumberland Cave deposit from those of the race of mink living in the same region today.

*Mustela vison vulgivaga* (Bangs)

*Putorius vison*, Brown (1908, p. 180, pl. 17); Osborn (1910, p. 488).

*Mustela vison*, Hay (1914, p. 32; 1924, p. 252); Hay (1930, p. 529, part).

*Lutreola vison*, Matthew (1915, p. 402).

*Remarks*—The citations to literature all refer to material taken from the Conard Fissure of Arkansas. From Brown's account (1908, p. 180, pl. 17) one learns that of the seven skulls and twenty-eight separate jaws found there, the longest skull measures 66 millimeters. This measurement, assuming that it is the condylobasal length, agrees well with Hollister's (1913, p. 474) measurements for *Mustela vison vulgivaga*, which subspecies probably inhabits the region today. At any rate the single Recent specimen available from the general region, a skull alone, No. 51607, Mus. Vert. Zool., from Boone County, Arkansas, seems referable to *vulgivaga*. However, the present writer has not examined the fossil material and his reference of it to the subspecies *vulgivaga* should be regarded as a tentative assignment and not as a definite subspecific identification.

*Mustela macrodon* (Prentiss)

*Lutreola macrodon* Prentiss (1903, pp. 887-888, fig. a); Loomis and Young (1912, pp. 27-28).

*Mustela macrodon*, Miller, G. S., Jr. (1912, p. 101); Hollister (1913, p. 478); Miller, G. S., Jr. (1924, p. 127); Hay (1930, p. 528).

*Lutreola vison antiquus* Loomis (1911, pp. 227-229, 2 figs. in text).

*Putorius macrodon*, Trouessart (1904, p. 206).

"extinct mink," Hardy (1903, p. 125).

*Remarks*—This big mink, known from remains taken from Indian shell mounds on the coast and coastal islands of Maine, has been included in Hay's list of fossil mammals with the suggestion that the beds from which it is known are Recent. Loomis (1911, p. 227) in proposing the name *Lutreola vison antiquus* overlooked the earlier name, *Mustela macrodon* of Prentiss (1903, p. 888). Shortly after Prentiss described this large mink Hardy (1903, p. 125) published information which indicates that it existed until about 1860 when it probably was exterminated by those who were seeking its fur. The writer has not examined specimens and follows Hollister (1913) in treating it as a full species rather than as a subspecies of *Mustela vison* as Loomis (1911) did.



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PLATE 1

*Brachyprotoma obtusata* Cope

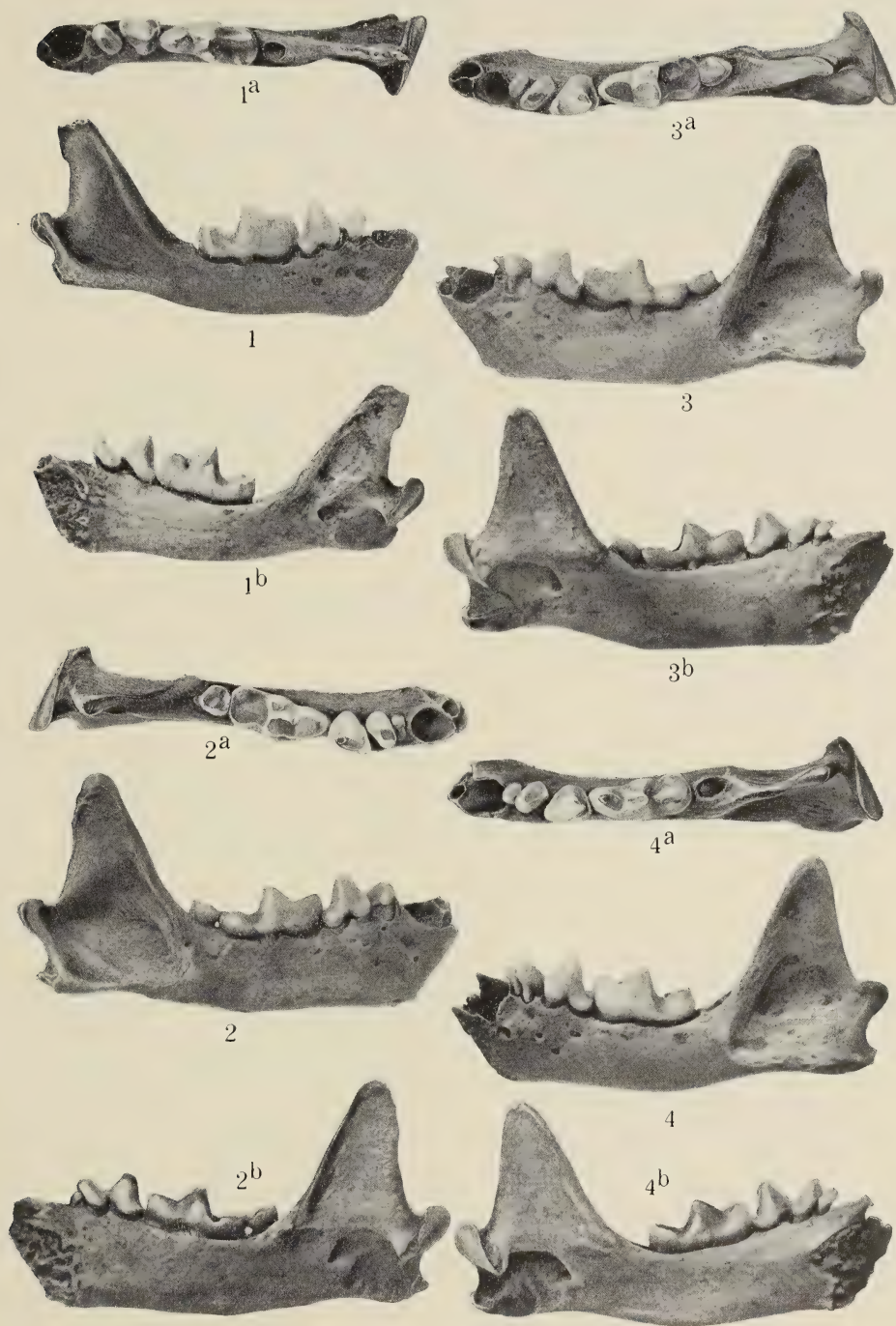
FIGS. 1, 1a, 1b—No. 12399, young, type-specimen of *Brachyprotoma spelæa* Brown.  
Three views of right lower jaw.

FIGS. 2, 2a, 2b—No. 11773, adult. Referred by Brown (1908) to *Brachyprotoma pristina*.  
Three views of right lower jaw.

FIGS. 3, 3a, 3b—No. 11773, adult. Referred by Brown (1908) to *Brachyprotoma pristina*.  
Three views of left lower jaw.

FIGS. 4, 4a, 4b—No. 11773, adult. Referred by Brown (1908) to *Brachyprotoma pristina*.  
Three views of left lower jaw.

All figures,  $\times 2$ . Amer. Mus. Nat. Hist. Coll. Pleistocene, Conard Fissure, Arkansas.



*Brachyprotoma obtusata* Cope



PLATE 2

*Brachyprotoma obtusata* Cope

FIGS. 1, 1a, 1b—No. 8214, U. S. Nat. Mus., subadult, Cumberland Cave, Maryland. Three views of right lower jaw.

FIGS. 2, 2a, 2b—No. 12045, U. S. Nat. Mus., adult, Cumberland Cave, Maryland. Three views of left lower jaw.

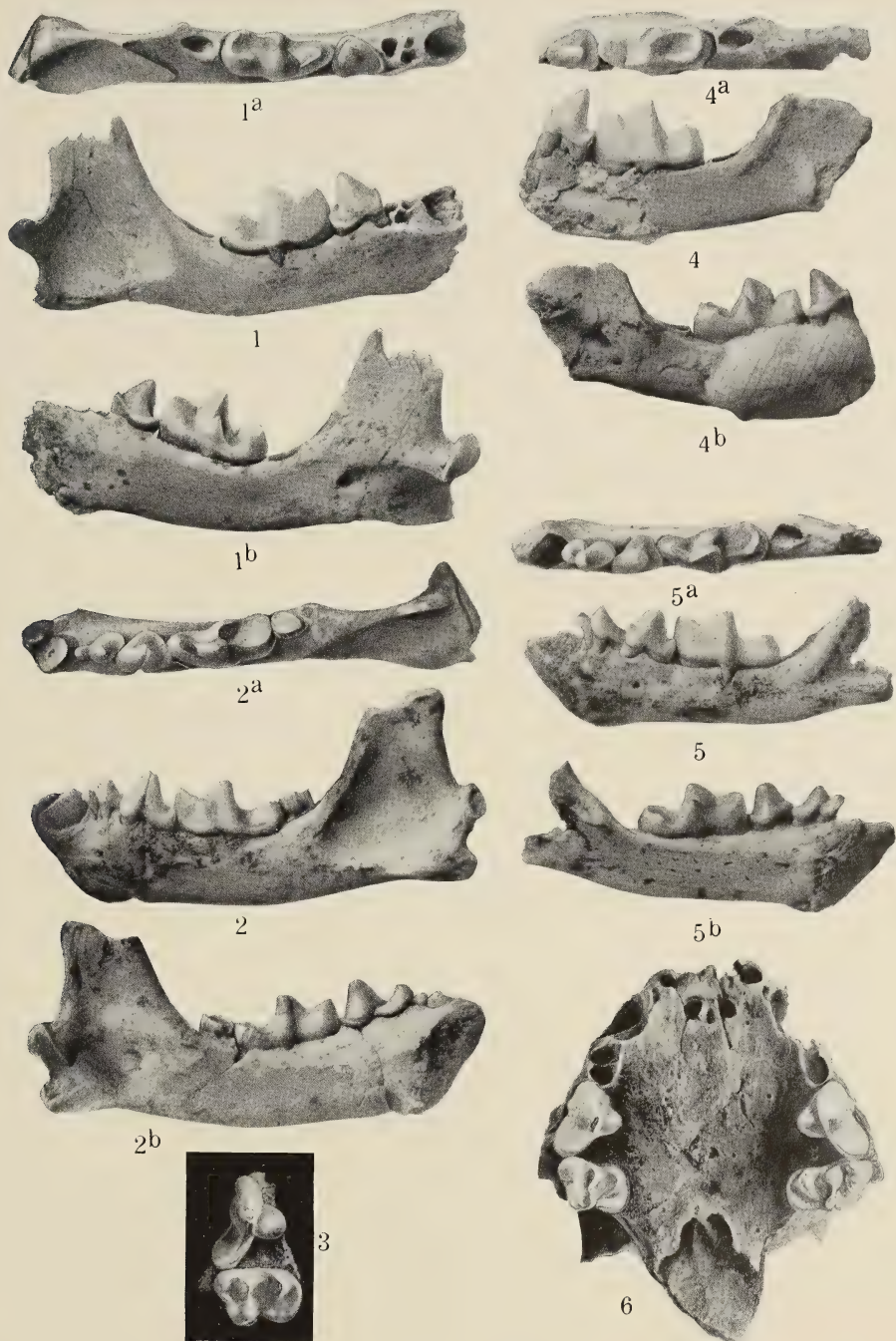
FIG. 3—No. 11057A, Carnegie Mus., adult, Frankstown Cave, Pennsylvania. Occlusal view of right P<sub>4</sub> and M<sub>1</sub>.

FIGS. 4, 4a, 4b—No. 8165, U. S. Nat. Mus., young, Cumberland Cave, Maryland. Three views of left lower jaw.

FIGS. 5, 5a, 5b—No. 12046, U. S. Nat. Mus., adult, Cumberland Cave, Maryland. Three views of left lower jaw.

FIG. 6—No. 12426, Amer. Mus. Nat. Hist., subadult, Conard Fissure, Arkansas. Type specimen of *Brachyprotoma pristina* Brown. Palatal view of anterior portion of skull.

All figures,  $\times 2$ .



*Brachyprotoma obtusata* Cope

PLATE 3

*Brachyprotoma obtusata* Cope

FIGS. 1, 1a, 1b—No. 11057, Carnegie Mus., subadult, Frankstown Cave, Pennsylvania. Three views of right lower jaw.

FIGS. 2, 2a, 2b—No. 11057, Carnegie Mus., subadult, Frankstown Cave, Pennsylvania. Three views of left lower jaw.

FIGS. 3, 3a, 3b—No. 11058, Carnegie Mus., young, Frankstown Cave, Pennsylvania. Three views of left lower jaw.

FIGS. 4, 4a—No. 11772, Amer. Mus. Nat. Hist., adult, Conard Fissure, Arkansas. Referred by Brown (1908) to *Brachyprotoma pristina*. 4, ventral view of skull; 4a, lateral view of right maxilla and teeth.

All figures,  $\times 2$ .





*Brachyprotoma obtusata* Cope

PLATE 4

The specimens of *Osmotherium* are all from the Port Kennedy bone deposit and are in the collections of the Academy of Natural Sciences of Philadelphia.

FIGS. 1a, 1b—*Osmotherium spelæum*, subadult No. 72.

FIGS. 2, 2a, 2b—*Osmotherium spelæum* Cope, adult, type specimen, No. 67.

FIGS. 3, 3a, 3b—*Mephitis mephitis estor*, Recent, No. 47141, Mus. Vert. Zool., young, Zion National Park, Utah.

FIGS. 4, 4a, 4b—*Conepatus mesoleucus mearnsi*, Recent, No. 32496, Mus. Vert. Zool., young to subadult, Chiricahua Mountains, Arizona.

FIGS. 5, 5a, 5b—*Osmotherium spelæum*, young, type specimen of *Mephitis orthostichus* Cope, No. 71.

FIGS. 6, 6a, 6b—*Osmotherium spelæum*, young, referred by Cope (1899) to *Mephitis leptops*, No. 75.

FIGS. 7, 7b—*Osmotherium spelæum*, young, type specimen of *Mephitis leptops* Cope, No. 75.

FIGS. 8, 8a, 8b—*Osmotherium spelæum*, adult, referred by Cope (1899) to *Mephitis orthostichus*, No. 73.

FIG. 9—*Osmotherium spelæum*, adult, type specimen of *Mephitis fossidens* Cope, No. 69.

FIG. 10—*Osmotherium spelæum*, young, referred by Cope (1899) to *Mephitis fossidens*, No. 70.

FIGS. 11, 11a—*Osmotherium spelæum*, adult, referred by Cope (1899) to *Mephitis fossidens*, No. 68.

All figures,  $\times 1$ .

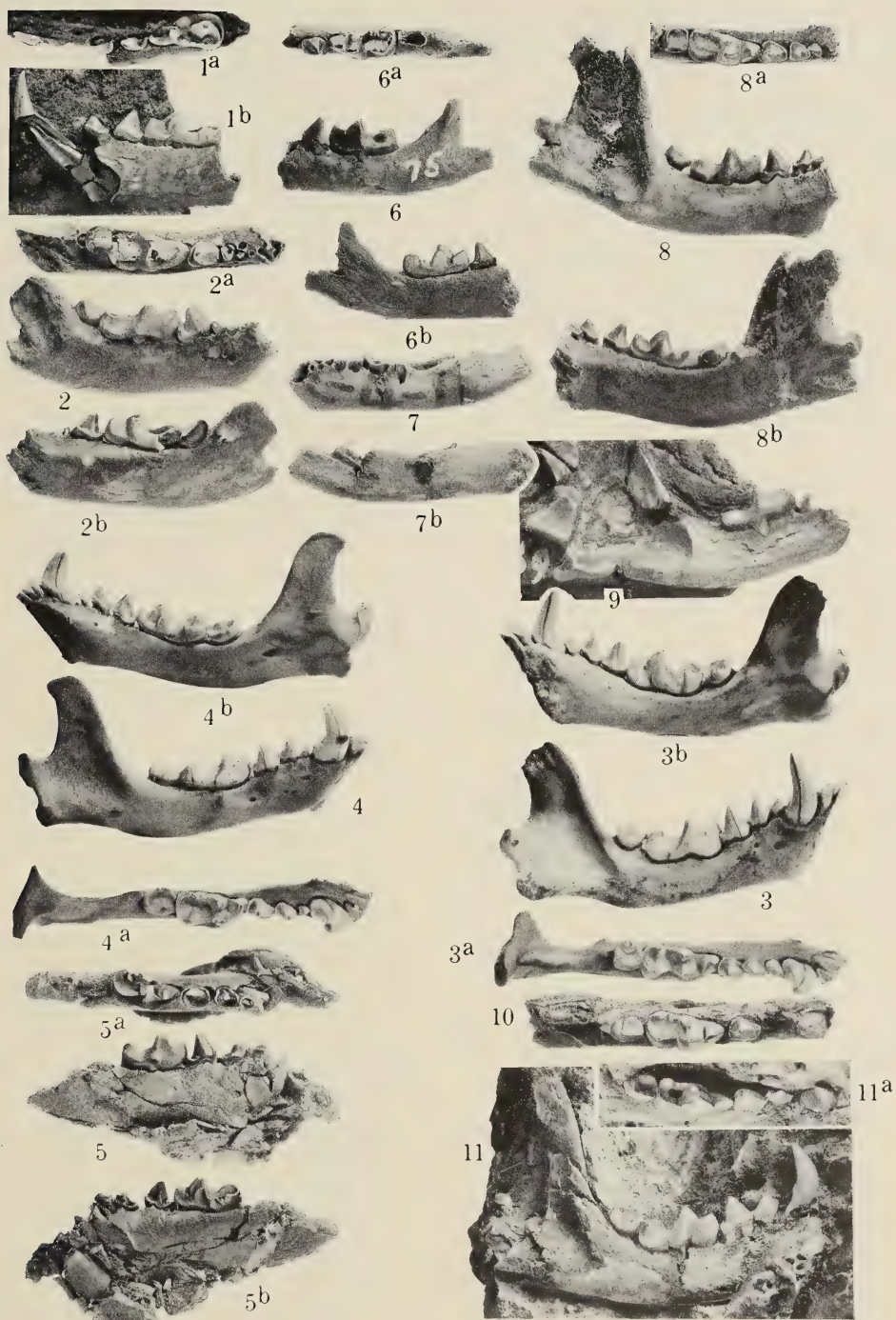




PLATE 5

FIGS. 1, 1a, 1b—*Mephitis mephitis nigra* (Peale and Beauvois). No. 2232, U. S. Nat. Mus., type specimen of *Mephitis frontata* Coues. 1, palatal view of skull; 1a, occlusal view of lower dentition; 1b, lateral view of right lower jaw;  $\times 1$ .

FIGS. 2, 2a, 2b—*Spilogale marylandensis* Gidley and Gazin. Type specimen, No. 12048, U. S. Nat. Mus., adult, Cumberland Cave, Maryland. Three views of lower jaw;  $\times 2$ .

FIGS. 3, 3a, 4, 4a—*Taxidea taxus berlandieri* Baird. Nos. 10209 and 10208, respectively, Val Verde Copper Mines, at Anita, 40 miles north of Williams and 20 miles south of the Grand Canyon, Arizona. 3, 3a. Internal and external faces of posterior part of right innominate bone; 4, 4a. Two views of left ulna, type specimen of *Taxidea robusta* Hay.  $\times 1$ .

FIG. 5—*Mephitis frontata* Coues. Lateral view of left side of skull of type specimen, No. 2232, U. S. Nat. Mus., to show abnormal tumidity of frontal region caused by infestation of frontal region with parasites;  $\times \frac{1}{2}$ .





















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